

CONTRIBUTIONS FROM THE LABORATORY OF VERTEBRATE BIOLOGY
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**A Geographic Study of the Herpetofauna of
Alta Verapaz, Guatemala**

by
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INTRODUCTION

In a previous paper (Stuart, 1948a) I presented a list of the amphibians and reptiles known to occur in the Department of Alta Verapaz, Guatemala. In the same paper a résumé of the geography of that herpetofauna was also given with the notation that a more complete account would be forthcoming. The following is the geographic analysis anticipated at that time.

The data set forth in this account were gathered in the course of twelve months of field investigations carried on during the years 1938 and 1940. Not all the time in the field was spent in exploring Alta Verapaz. Studies were made in the desert basins to the south (Schmidt and Stuart, 1941) and in the Sierra de los Cuchumatanes to the west (Stuart, 1943b), and in the autumn of 1944 a brief survey of Guatemala as a whole was undertaken. It has been through these investigations of adjacent areas that the establishment of the faunal regionality of Alta Verapaz has in large measure been made possible.

In all some 2200 specimens (exclusive of tadpoles) from Alta Verapaz

have been studied, and an examination of many more has been necessary in order to untangle a multitude of taxonomic problems. Most of the specimens upon which this study is based were collected by me, so that field observations on habits, habitats, and ecological interrelations have been possible.

From faunal Alta Verapaz 129 forms (species and subspecies) have been recorded, divided among sixty-eight genera. Of these forms I have collected 113 and have examined eleven others which were not seen in the field. Only five species reported from Alta Verapaz have not been seen by me, and these are preserved in the collections of European museums. Alta Verapaz has served as the type locality for sixty-nine amphibian and reptilian forms of which I recognize forty-seven as valid.

As those familiar with the tropics know well, a large species list gives no indication of the abundance of any single form. In many instances only one or two specimens of some species were collected. As a result it is difficult to present a correct picture of the distribution of many forms. The following account, therefore, can serve as little more than a preliminary statement of the geographic complex. It is believed, however, that even though continued work in the area may result in the refinement of certain of my conclusions, sufficient data have been made available to establish rather firmly my broader generalizations.

In further apology for the shortcomings of this paper, I acknowledge myself guilty of an exposition in which I do not wholly believe. Because amphibians and reptiles have been grouped together, it has been customary for herpetologists to attempt geographic summations of these two diverse groups viewed as a unit and as comprising a herpetofauna. With the possible exception of some few amphibians which have been able to divorce themselves from the aquatic environment, the life requirements of the two classes are so utterly different that any similarity they may show in the details of their respective geographic patterns must be largely fortuitous. Proof for this viewpoint with respect to the herpetofauna of Alta Verapaz will be brought out shortly. In my opinion, however, it is time that herpetologists face the enigma with which they have been confronted and throw overboard the unnatural faunal alliance with which they have been saddled. Only my conservatism and respect for tradition have prohibited me from taking such a step at this time.

Since my previous paper (Stuart, 1948a) contains the fundamental data upon which this study is based, a condensation of that material, that is, a faunal list and geographic summary, is given in Table I (page 22). In addition to data already presented, many of the conclusions set forth are founded upon unpublished data on habits, detailed ecology, local abundance, and the like gathered in the course of my field investigations. For data concerning the sources of collections, locations, and itineraries the reader

is referred to my previous account. Despite certain recent nomenclatorial changes, I retain here the allocations made in that report (1948a).

On the basis of its salamander fauna the major part of Alta Verapaz constitutes a distinct faunal area, which has been designated the Quecchian biotic province (Stuart, 1942 and 1943a), and an examination of the region's entire herpetofauna supports that contention. Some modification of earlier conclusions must, however, be admitted. I believe now that I was hasty in calling "biotic provinces" the Guatemalan regions previously outlined. That they constitute faunal areas with reference to amphibians and reptiles I am fairly certain, but to have expanded them to include an entire biota was unwarranted. As knowledge of Central America has increased, it has become apparent that those regions, even were they truly biotic in nature, do not parallel the biotic provinces of North America as set forth by Dice (1943). It is not improbable that, biotic or merely faunal, several will eventually be reduced to the stature of "districts" (*sensu* Dice).

For that reason what were previously called "biotic provinces" will in the following be referred to as "faunal areas," with the understanding that the herpetofauna alone is being considered. Furthermore, my use of the term "faunal area" is purposely loose, and it should not be thought of as being a part of any particular zoogeographic system. In fact little evidence supports any previously suggested concept as an expression of the distribution of the Guatemalan herpetofauna. Dice's biotic province hypothesis is herein accepted in part, as my data lend support to it more than to any other zoogeographic system of classification.

Although the subject will be treated in more detail later, it may be noted here that a zoogeographic analysis of northern Central America is rendered difficult owing to the complexity of both environment and fauna. The geological history of the region and more especially that of adjacent areas indicates that the nuclear upland has been subjected to alternate periods of connection and isolation from the land masses to the north and the south. This situation has permitted successive faunal elements to invade northern Central America and has facilitated, at the same time, the development of an autochthonous element. Several elements have then combined to produce distinct faunas, and these have intermingled and further differentiated to produce assemblages in the diverse environmental units. These assemblages characterize the numerous faunal areas too little known to be evaluated properly.¹

This distinction between fauna and area is adhered to in the following. In this account the approach is regional in that a region's fauna is treated. Naturally, the establishment of regionality and the blocking out of minor ecological units within the area as a whole proceeds through an analysis of

¹ The terms "element," "fauna," "assemblage," etc., as herein used, have no special connotation. All refer to a simple faunal unit without any reference to size and are at times used synonymously.

faunas. Thus, the two concepts may seem occasionally to merge into one. Once regionality of Alta Verapaz² has been established and a description of the distribution of the fauna has been presented, the interpretation and the conclusions drawn therefrom are presented from the faunal point of view.

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My way in Guatemala was made smooth by the generous co-operation of the Carnegie Institution of Washington, especially through the Director of Historical Research, Dr. A. V. Kidder, and the staff of his Guatemalan office. The various officials of the Republic of Guatemala were most courteous in extending to me many privileges not ordinarily afforded *extranjeros*.

During my field investigations I was fortunate in receiving the hospitality of many individuals in Guatemala, and my work there was greatly simplified through their interest and helpful suggestions. I wish especially to mention Mrs. R. W. Hempstead of Cobán and her sons Allen and the late Robert. Their numerous fincas were always at my disposal, and my memories of Alta Verapaz will always center around their warm hospitality. The home of my friends, the late Mr. William Bird and Miss Edith Baker, also of Cobán, was always mine. At Finca Volcán I was entertained by Mr. Reginald O'Donnell and his wife. Mr. and Mrs. Gustav Helmrich of Finca Samac and the late Mr. and Mrs. George Appenzauser, formerly of Finca Panzamalá, were all most generous hosts. While I was working from Panzós, Mr. John ("Smitty") Casprowitz and Mr. Herbert Dröge, both lately of that village, made an otherwise unpleasant locality most livable, and my work in the lower Cahabón Valley was made possible through the efforts of Sr. don Anastacio Chiquín B. of Finca Canihor. The eminent Maya authority, the late Mr. Erwin P. Dieseldorff, of Cobán, supplied me with many data and many suggestions which greatly furthered my investigations. These and many others who supplied me with lodgings and *mozos* at other stations, or who welcomed me for refreshments along the trail, rendered what was often difficult country comfortable and made my way easy.

² Since the Quechian faunal area almost coincides with the Department of Alta Verapaz, the two names will be used interchangeably.

In assembling and interpreting data my colleagues at the University of Michigan have been most generous with their time and knowledge, especially Dr. Lee R. Dice, Dr. Norman E. Hartweg, and Dr. Charles F. Walker. I have had the benefit of the knowledge of the Middle American authorities, Dr. Edward H. Taylor, of Kansas University, Dr. Hobart M. Smith, of the University of Illinois, and Dr. E. R. Dunn, of Haverford College. I have been particularly fortunate in having had the privilege of corresponding with Mr. Karl P. Schmidt, of the Chicago Natural History Museum. His broad experience in Guatemala and adjacent regions he unselfishly placed at my disposal. He has been kind enough to labor through the first draft of this paper and to offer me his valuable criticisms. Mr. Paul Standley and Dr. Julian Steyermark, both of the Chicago Natural History Museum, have critically reviewed the notes on the vegetation of Alta Verapaz. To all of them I wish to express my sincere gratitude for their courtesies, aid, and advice.

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NATURAL LANDSCAPE

The following account of the physical geography of Alta Verapaz is little more than a résumé of the detailed accounts of Sapper (1902, 1932, and 1937) and the descriptions of Termer (1936). Although there is still much to be learned of the geology, climate, and vegetation of the region, in their broader outlines, Sapper's studies will always serve as a basis for further refinements. Throughout the following account I have applied his geographic nomenclature to somewhat more extensive areas (that is, the Sierra de Xucaneb to include the entire middle mountain mass of Alta Verapaz) and have occasionally invented such names as "Meseta de Cobán."

Geology and Physiography

Physiographically, Guatemala may be viewed as a highland mass surrounded on three sides by lowlands. The nucleus of this area is the broad Guatemalan plateau with a northwest to southeast trend, occupying most of the western and southern third of the country. From this plateau three arms of mountains extend eastward towards the Caribbean. In the north lies the Cuchumatán-Alta Verapaz mountain province, farther south the Chuacús-Minas-Mico range, and along the Honduran border the Sierra de Merendón and associated ranges. These three chains are separated by

the Ríos Negro-Polochic depression and by the valley of the Río Motagua, respectively. On the south and west of this entire area lies the Pacific coastal plain, while the Caribbean lowlands border it on the north and east. On the south and east the Guatemalan highlands continue into the Honduran mountain chains.

In this picture, Alta Verapaz, comprising some 8600 square kilometers, represents the eastern end of the more northern mountain arc of Guatemala and is separated from the Sierra de los Cuchumatanes by the deep gorge of the Río Negro. It is little more than a secondary ridge on the northern slope of the eastern Chuacús-Minas-Mico range (Sapper, 1902: 96) from which it is separated by the Polochic-Panimá valleys, except for a highland bridge at its western end between the headwaters of the Polochic drainage system and that of the Río Negro.

The Chuacús-Minas-Mico arc arose as a folded mass before the Carboniferous period, and it has determined, to a large extent, the trend of the younger system to the north. This latter area was flooded during the Carboniferous (possibly lower Permian), Cretaceous, and Miocene by seas of decreasing extent, the last barely reaching the northernmost border of Alta Verapaz. The beds thus produced were folded and faulted along an east-west axis during the Pliocene orogeny to produce the Cuchumatán-Alta Verapaz mountain arc. Thus, east of the Río Negro gorge, a highland mass was raised, dipping toward the north and plunging eastward, which subsequent faulting divided into four orographic zones. This faulting occurred only in the eastern part of the area to form the Polochic-Panimá valleys just north of the Sierra de las Minas and the Cahabón Valley farther north. An unbroken western highland mass was thus produced from which three lesser mountain arcs extend toward the east: a mountain range between the valleys of the Panimá and the Polochic, a second between the Polochic and Cahabón valleys, and a third north of the Cahabón. These orographic zones may be known as the Meseta de Cobán, Sierra de Pansal, Sierra de Xucaneb, and Sierra de Pocolhá, respectively (Map 2).

The Meseta de Cobán or the Cobán tableland remained unbroken by block faults and stands as an elevated plateau some 1200 m. high, dominated by small ranges reaching 2000 m. (Pl. VII, Fig. 1). The heavy rainfall of the region has caused much erosion so that ranges of low, possibly residual, hills make its surface extremely rugged. From it, as the backbone of Alta Verapaz, the Xucaneb range extends eastward. This upland mass reaches isolated elevations of about 2500 m. (Cerros Chichén and Xucaneb) in the west, but at its eastern end, where it breaks up into several smaller ranges in the region of Senahú, it does not rise above 1500 m. From the southern end of the Meseta de Cobán the short Sierra de Pansal, which exceeds 2000 m. elevation only locally, extends eastward to the confluence of the Ríos Panimá and Polochic. The Pocolhá range reaches out from the

northern end of the Meseta de Cobán and does not exceed 2000 m. in the west; to the east it remains below 1200 m. These ranges are complex folds, and the last named, particularly, is made up of a series of east-west "ground waves" decreasing in height toward the north (Pl. I, Fig. 1) and disappearing entirely in the region of Chisec. The northward dip and eastward plunge of these ranges play a major role in the climatic pattern of Alta Verapaz which largely determines the biotic subdivisions of the area.

The lowlands of Alta Verapaz may be divided into four units. Most extensive are the Caribbean lowlands, which make up the northern half of the province and border it on the east, where they merge with the lowlands of the Polochic Valley. To the east they are seasonally flooded by the Río Polochic (Pl. III, Fig. 2); to the north the low steplike ridges often produce incomplete drainage in the intervening depressions and extensive marshy areas are developed, as, typically, in the region between Samanzana and Chisec (Pl. III, Fig. 1). The Pansal, Polochic, and Cahabón valleys are depressions within the main highland area. All appear to be rift valleys. The Río Polochic has its headwaters just east of Tactic and flows almost due east in a narrow V-shaped gorge west of La Tinta. Between its source and La Tinta (35 km.) the river falls about 1200 m. Below La Tinta, at the confluence with the Río Panimá, it spreads out over an extensive flood plain which at Panzós is over 10 km. broad (Pl. I, Fig. 2). The Río Panimá parallels the Polochic above La Tinta and occupies a steep-sided gorge almost throughout its course.

The Río Cahabón also rises in the Tactic region, but flows northward across the Meseta de Cobán. At Cobán it turns eastward and east of San Pedro enters the western end of the Cahabón rift. It occupies a narrow gorge until near Xicacao where, though the river remains entrenched (Pl. V, Fig. 1), its valley begins to broaden and finally reaches its greatest width at Cahabón, where it is some 10 km. broad. This valley is not level but, like the Cobán tableland, is broken by ranges of low hills. Within the rain shadow of the Pocolhá range, this valley is subhumid, and few tributaries enter the main stream. East of Cahabón the river turns southward, cuts through the relatively low eastern end of the Xucaneb range, and enters the Río Polochic east of Panzós.

Bordering the Quecchian faunal area on the west and southwest is the gorge of the Río Negro. It extends from its confluence with the Río Rabinal to Providencia in a great S-shaped loop. This deep and narrow entrenchment is a part of the Zacapan faunal area to the south of Alta Verapaz.

The mountains of Alta Verapaz, being largely limestone and subjected to heavy precipitation, have the features of karst topography. Most striking of the topographic forms are the small, knobby hillocks, which rarely exceed 100 m. in altitude. These are arranged either in short series or are scattered haphazardly over the area. They are most conspicuous on the

Meseta de Cobán and in the Cahabón Valley, where vegetation is somewhat sparser, but they occur on the northern lowlands and on the crests of both the Xucaneb and Pocolhá ranges. So numerous are these hillocks that level stretches of terrain in Alta Verapaz constitute an unusual sight, and plain surfaces of a few acres extent are most infrequent.

Despite the abundance of surface water, much of the drainage in Alta Verapaz is subterranean. Surface streams often disappear into rocks, only to reappear again as springs in other areas. Not infrequently one can hear the trickle of subterranean streams beneath one's feet, especially in the wet season.

Solution, playing as it does so large a role in this wet limestone country, has produced numerous caves and sinks. These sinks, commonly known by their Quecchi name, *sigüans*, are common features and range in size from a foot in diameter to, as west of Samac, large enough to contain a farm. They are generally of great depth with sheer walls and in uncleared land render travel most hazardous (Pl. IV, Fig. 1). The almost complete absence of surface water locally is of the utmost importance to the distribution of amphibians.

Soils of Alta Verapaz are largely residual, laterite-like clays. The relief of the area as a whole precludes any great development of a soil mantle except in the valleys. The mountain slopes have a very thin soil mantle, and the small hillocks are often completely without soils. In spite of this, coffee maintains a firm footing on the very steepest slopes, and even on almost bare rock the tropical and subtropical forest trees seem to flourish. On the lowlands, alluvial material forms deep soils which are particularly well adapted to corn and cacao culture and, in virgin country, support a high forest.

Climate

The tremendous relief of Alta Verapaz produces not only considerable climatic variations but delimits the extent of these variations along remarkably sharp boundaries. Temperature within the region depends on the altitude; moisture depends primarily upon the trade winds and secondarily upon the orography of the region.

The widespread and loosely recognized vertical temperature belts, *tierra caliente*, *tierra templada*, and *tierra fria*, of Latin America, are useless as expressions of climatic details. According to an analysis of vertical temperature gradients in Alta Verapaz, temperature averagely decreases about 1° C. per 200 m. increase in elevation. At sea level the average annual temperature is probably in the neighborhood of 25° C., with a variation of possibly 6° to 7° C. between the coldest (December) and warmest (May or June) months. At higher elevations the annual variation in temperature is somewhat reduced. At Cobán (1300 m.) the annual mean is about 18° C., the coldest month 16° C., and the warmest about 20° C. The most

important temperature break appears along approximately the 1300 to 1500 m. contour above which occasional frosts are first recorded.

The herpetofauna of Alta Verapaz is arranged into three vertical belts, with the most distinct faunal break occurring along the 1300 to 1500 m. contour. A second and less distinct boundary lies in the neighborhood of the 600 m. contour. It is suggested, therefore, that three vertical temperature zones, discussed in greater detail later, be recognized, which, while probably of little importance in a classification of temperature, may prove of value as faunal limits. These are:

Tropical zone. Frost free. 0-1300 m.

Lower division. 0-600 m.

Upper division. 600-1300 m.

Subtropical zone. Zone of frosts. Above 1300 m.

The rainfall of Alta Verapaz, owing to the tremendous relief of the region, varies considerably geographically and may be characterized as "seasonal." From mid-May through November possibly 80 per cent of the annual precipitation falls. This is the "winter" season; the "summer" extends from about December to mid-May.

Generally speaking, the north- and east-facing (windward) slopes are excessively humid, whereas the south- and west-facing areas lie in a rain shadow and though humid receive not more than half the precipitation of the windward slopes. The region of greatest rainfall is the northern lowlands and adjacent slopes of the Pocolhá range, which in many places receive in excess of 5000 mm. of rainfall annually. To the south of this low range the Meseta de Cobán receives only about 2500 mm. of rainfall and the mountain-encircled Cahabón Valley east of the Meseta probably receives no more than 1500 mm. The northern slopes of the Sierra de Xucaneb above approximately 1000 m. escape the rain-shadowing influence of the Sierra de Pocolhá and are excessively humid. Up to 4000 mm. of precipitation have been recorded at stations of about 1300 m. elevation, and at higher elevations the perpetual cloud blanket suggests even more humid conditions.

The Panimá-Polochic depression and the adjacent mountain slopes lie entirely within the rain shadow of the Sierra de Xucaneb. Though local winds from the east supply the lower valley with as much as 5000 mm. of rainfall, the western upper end of the depression, where it adjoins the Meseta de Cobán, receives less than 3000 mm.

Four rainfall zones may be recognized within faunal Alta Verapaz; a lowland and a highland humid zone, a lowland and a highland zone which is somewhat drier and which, though it is not strictly correct, may be referred to as subhumid. Combined with the temperature zones previously noted, the climatic pattern of Alta Verapaz may be arranged as follows:

Tropical zone. 0-1300 m.

Lower division. 0-600 m.

Humid belt—northern and eastern lowlands

Subhumid belt—Cahabón depression

Upper division. 600-1300 m.

Humid belt—Sierra de Pocolhá, Sierra de Xucaneb,
and Sierra de Pansal

Subhumid belt—Meseta de Cobán

Subtropical zone. Above 1300 m. Sierra de Pocolhá,

Sierra de Xucaneb, Sierra de Pansal, local hills above

Meseta de Cobán surface.

Vegetation

Though hardly acceptable to a botanist, the following treatment of the vegetation of Alta Verapaz seems adequate for my purpose. The classification of the cover types presented is based upon the physiognomy of the cover, which is, in all probability, its main relationship to the herpetofauna. With but slight modification the classification of Sapper (1902) has been employed. In a very real sense the cover represents a summation of climatic conditions and departs therefrom only locally, wherever edaphic conditions produce minor departures from the generalized climatic control. As will be noted later, the pattern of the major cover types coincides closely with that of the herpetofauna.

Five vegetational zones may be recognized:

Tropical zone

Lower division

1. Broadleaf forest

2. Savannas

Upper division

3. Broadleaf forest

4. Pine forest

Subtropical zone

5. Cloud forest

The broadleaf forests of the lower division of the Tropical zone are restricted to all those parts of Alta Verapaz lying below about 600 m. with the exception of the valley of the Río Cahabón. This is the forest generally referred to as the "corozo belt" in which the corozo palm, mahogany, and rubber are characteristic. Whether this broadleaf forest is sufficiently different to warrant separation from that between 600 to 1300 m. I am unable to say (the virgin forests of the two are similar in appearance), but as conditions exist today, the two belts are distinct.

The corozo belt, as here defined, includes the eastern and northern lowlands to the upper limit of the corozo palm and the lower limit of intensive coffee cultivation. Over most of Alta Verapaz this belt was probably orig-

inally covered with rain forest, but cultivation has modified the virgin condition.

In the very humid northern lowlands the two major forest types appear to be the upland type and that which occupies poorly drained depressions. The uplands have a high forest, often exceeding 50 m., with a dense roof which permits little light to reach the forest floor. This produces a rather open condition within the forest, though there is an abundance of bromeliads and climbing types as well as many smaller species growing on the floor itself. The depressions which are extensively inundated during the prolonged wet season support a very different forest. The more widely spaced dominant hardwoods permit more light to reach the forest floor. This much denser forest supports a rank underlayer of ferns and palms.

The forest of the eastern lowlands appears much dryer than that of the north. Though the Río Polochic annually floods most of the area (Pl. III, Fig. 2), the waters recede rapidly as the river falls, and the dry season is much more severe than it is in the north. The virgin forests of the Polochic Valley are of a more deciduous type than are those of the north. Many of the trees shed their leaves during the dry season. The light which penetrates to the forest floor permits a heavy undergrowth to develop, and the resulting forest is much denser than that of the well-drained uplands of the north.

Along the water courses both on the northern and eastern lowland the vegetation is extremely heavy. Beneath the high forest along the water's edge grows a dense thicket of low bushes and grasses which render herpetological collecting extremely difficult. Throughout the region the high virgin forest is known as *montaña*.

Clearings in the virgin forest are of several types. The first, for pastures, are more or less permanent. In such areas grasses and low shrubs predominate and continuous grazing does not permit the reinvasion of the forest. The second type, for subsistence farming (corn, chiles, beans), is utilized for shorter periods (Pl. II, Fig. 2). After several years of planting, the land is allowed to lie fallow. Within a year grasses and low plants have taken it over, and after several years it supports a rank growth of bushes, vines, and low trees (Pl. II, Fig. 1). If allowed to remain undisturbed it will gradually be reclaimed by the forest, but it is general practice to reclear the land after a few years for further planting. This system of milpa agriculture, as it is called, has been well described by Lundell (1937) and many other authors. The various stages of the rank second growth are known as *monte* as opposed to the *montaña* described above. A few areas in which rubber or cacao are cultivated are, like the pastures, more permanent. Within such groves conditions are roughly comparable to those of the virgin forest.

A notable departure from this generalized broadleaf forest of the corozo

belt is found in the valley of the Río Panimá, in which pine and pine savannas occur. Cook (1909: 20) suggested that this pine is a subelimax type. Insofar as the fauna of this region is concerned, it supports species typical of the rank second growth of the lowlands.

On the northern lowlands, virgin forest is still extensive, and clearings are scattered. On the eastern lowlands of Alta Verapaz, virgin forest is a rarity. Practically the entire Polochic Valley below La Tinta to the Yzabal border has been extensively cleared, and the second growth of grasses and low bushes is dominated by the abundant corozo palm and scattered ceiba trees (Pl. I, Fig. 2). The only extensive virgin forest in the region lies south of the Río Polochic below Panzós.

The savannas of the Tropical zone occur in the Cahabón Valley east of the level of about Finca Sasís. There is some question as to whether these pine savannas represent virgin conditions or have been produced by intensive cultivation. Cook (1909: 15) suggested that frequent burning has prohibited the development of a humid broadleaf forest, but Sapper (1902: 137) believed that, lying as it does in the rain shadow of the surrounding mountains, this depression is too dry to support humid forest growth. Certain faunal elements, as will be shown, support Sapper's viewpoint. Regardless of their origin, these pine savannas now cover the region. Where cultivation has not been practiced for some time, tall grasses, scattered pine groves, and the stunted *nance* and *sahá* trees are the dominant floral types (Pl. V, Fig. 2). Along the larger watercourses, a narrow belt of broadleaf forest has often developed (Pl. V, Fig. 1). As the Meseta de Cobán is approached, rainfall probably increases, and thickly undergrown pine groves are more frequent than they are in the Cahabón region.

Much of the valley is under intensive cultivation. Corn is extensively planted, and considerable cacao has recently been grown along the watercourses. The district was formerly famous for its fine cotton. Where cornfields have been abandoned the typical second growth found in other regions is a conspicuous feature.

The upper division of the Tropical zone is within that region commonly referred to as the "coffee zone." In Alta Verapaz this coffee zone supports two very distinct vegetation types. The mountain slopes are predominantly in broadleaf forest, whereas the Meseta de Cobán is largely covered with pine.

Today little of the virgin broadleaf forest remains, most of it having been cleared away to make room for coffee plantations. This is particularly true of both slopes of the Sierra de Xucaneb and the Sierra de Pansal, as well as the south slope of the Sierra de Pocolhá. The north face of the Sierra de las Minas is, however, largely virgin, and the northern slopes of the Sierra de Pocolhá, owing to their distance from the main coffee outlets, have not been extensively cultivated.

On the face of the Sierra de Pocolhá, where precipitation reaches some 5000 mm. a year, the rain forest attains its maximum development, and the same may be true of the north face of the Sierra de las Minas. Both slopes of the Cahabón Valley and the Polochic face of the Sierra de Xucaneb are somewhat dryer. Where I have collected in the virgin forest of these areas, the vegetation was quite similar in appearance to that of the forest of the eastern lowlands (Pl. VI, Fig. 1). On the steep slopes of the Polochic Valley above La Tinta, pine, possibly owing to some edaphic factor, is more common than are broadleaf types.

Where the forest has been cleared away, the greater part of the land is planted in coffee (Pl. VI, Fig. 2). These coffee groves, known as *cafetales*, produce conditions intermediate between the forest and second growth. The coffee trees are planted fifteen to twenty feet apart and are interspersed with banana plants, which form a light shade. Such conditions provide a habitat similar to that of the lowland second growth. Some planters, preferring more shade in their groves, do not clear away all the larger trees. In such areas light is decreased and more humid conditions prevail, thus producing a habitat more like the virgin forest.

A feature of the coffee groves which plays a rather important role in reptilian distribution is its deep humus layer. This humus is formed as a result of the cleanings to which the groves are subjected several times each year. On many plantations it is the practice to rake the cut underbrush into piles which decay rather rapidly to produce an excellent habitat for many secretive species (Pl. IV, Fig. 2).

The coffee belt is not entirely planted in coffee. There is much land set aside for the cultivation of subsistence crops and for pastures. These clearings and the various stages associated with their abandonment are like those described for the corozo belt.

Although a center of human occupation for many centuries, tracts of virgin pine are still to be found on the Meseta de Cobán (Pl. VII, Fig. 1). These pine forests, in which pine, liquidambar, and oak are conspicuous, generally occupy the ridges and crests of the knobby limestone hills, whereas the more level areas between the hills are given over to cultivated land. The virgin tracts contain fine mature trees beneath which is a heavy undergrowth that in places becomes extremely dense (Pl. VII, Fig. 2 and Pl. VIII, Fig. 1). Along the streams on the Meseta the pine is replaced by broadleaf forest similar to the cloud forest. This "pine belt" (I shall hereafter refer to it as such in order to differentiate from the coffee belt described previously) becomes dryer to the east and gradually grades into the pine savannas of the Cahabón Valley. To the west and north local tongues of the Xucaneb and Pocolhá ranges cause the pine forests to break off somewhat more abruptly. Southward beyond the Pansal range the dryer conditions are less favorable for undergrowth and pine parklands appear.

Still farther south, beyond Santa Rosa, the pine forests are replaced by a pine-oak cover.

Where clearing has taken place on the Meseta, cornfields, coffee groves, sisal fields, and pastures are prevalent features. Inasmuch as agriculture in this area is conducted on a more intensive and better-managed scale, abandonment of the clearings occurs for only short intervals, so that the rank second growth, frequent in the Tropical zone, is rarely well developed.

The Subtropical zone, except for occasional small areas, supports the humid cloud forest. Although its lower limits vary from place to place, the 1300 m. contour may be taken as its generalized boundary. It is found on all four mountain ranges and on the higher isolated blocks rising above the Meseta de Cobán (Pl. VIII, Fig. 2). Only relatively small parts of the Sierra de Pocolhá attain sufficient altitude to support this vegetational type, and I have never visited the cloud forests of that range. For the most part these forests are virgin, since coffee yields in Alta Verapaz above 1300 m. are low, and the Indians prefer lower elevations for their cornfields.

In general, it is a broadleaf forest though Sapper (1902: Karte 5) indicated several sizeable stands of pine in this belt. The forest is extremely humid, being as a general rule overhung by cloud banks. It is dominated by large trees whose trunks are overgrown with a thick layer of moss (Pl. IX, Figs. 1 and 2). Though tree ferns are abundant beneath these larger trees, the cloud forest is fairly open. The ground is covered with ferns, bromeliads, and other low plants, and Dr. Steyermark of the Chicago Natural History Museum has informed me that it possesses one of the richest floras of Guatemala. Bromeliads are particularly abundant on the trees. The forest floor itself, owing to the low temperatures, is covered with a relatively deep layer of very wet humus. The few abandoned clearings in this belt support an extremely dense second growth.

GEOGRAPHY OF THE HERPETOFAUNA

Any complete zoogeographic description should include three separate though closely co-ordinated analyses: the faunal analysis, which merely describes the components of the faunal unit and which essays the establishment of that unit as an entity; the historical analysis, which attempts to explain how the unit arose; and the ecological analysis, which would explain why the unit exists or has existed as an entity. The first utilizes the tools of the systematist, the second must in a large measure call upon the techniques of the geologist and paleontologist, and the third borrows from the physiologist and morphologist.

That the three analyses should be closely co-ordinated is obvious. Many of the problems confronting the systematist can be interpreted only through the use of the geological and paleontological record. Again, the incomplete record of the past often necessitates, unwarranted in many instances

perhaps, the use of extant ecological information in an effort to reconstruct the historical aspects of the description.

In the case at hand, the meager data at our disposal preclude any possibility of such a complete description. At best the Alta Verapaz herpetofauna can merely be described and its unity established by comparing it with that of adjacent regions. Through a knowledge of local distributions of the various species and through an examination of the geological record and the phylogenetic relationships of some of the systematic groups one may further speculate on the origin of that faunal unit. But, lacking data on the adaptive morphology and on the physiological responses of the various components of the herpetofauna, any attempt to explain the "why" of observed geographic patterns must be relegated to the future.

The following account, therefore, will be concerned largely with a description of the Alta Verapaz herpetofauna, its local distribution, and a preliminary statement of its history. In a lesser measure, the interpretation of a few observed ecological relationships may contribute to an understanding of the broader geographic complex, and for this reason a brief discussion of some of the environmental factors, with which zoogeographic patterns appear to be correlated, is not out of place.

Factors Affecting Distribution

The geological features of the environment through their direct effects in producing pathways for dispersal, local isolation, and associated phenomena, and through their secondary effects upon climate, vegetation, and hydrography, have played a dual role in producing zoogeographic patterns in Alta Verapaz. In the course of examining the effects of geological history upon the distribution of a fauna it is well to recall Gadow's (1913: 13) now classic statement: "The key to the distribution of any group lies in the geographic configuration of that epoch in which it made its first appearance."

As a corollary it follows that the key to the composition of a region's fauna is in the geological history of that region. Although a full consideration of the direct distributional effects of geology will be presented later, it may be noted that the presence or absence of various faunal elements in Alta Verapaz must be interpreted first on the basis of past geological events and secondarily on paleoecological conditions which can only be surmised. Since Alta Verapaz, with all of nuclear Central America, has been a positive mass throughout the Cenozoic, it has served as a refuge for many of the older types which have apparently invaded the until recently inundated lowlands of the Yucatán Peninsula. Again the development of the Río Negro gorge may have produced partial isolation of Alta Verapaz from the plateau to the west. It is natural then that the fauna of the region, despite its upland nature, should now be more closely associated with that of the

low-lying Yucatán Peninsula to the north than with that of the western highlands. Furthermore, endemic forms derived from the west are more greatly differentiated from their stem species than are those which have recently invaded the uplands from the recently emerged lowlands.

The distributional effects of topography and relief are more conspicuous and better established than are those of the grander geological features. Topography is largely responsible for the climatic variations within the region. Temperature, for instance, is a function of altitude, whereas the distribution of land forms is a controlling factor of precipitation. The subhumid condition of the Cahabón Valley, to cite but one example, is due to the encircling mountains which shield it from the moisture-bearing winds. Climatic effects will be treated below.

Both geological structure and relief produce pronounced effects upon the hydrography of Alta Verapaz. The presence or absence of surface water is the major feature. The humid cloud forest might be expected to support a fairly large amphibian fauna, yet I found few species there. Karst development in that limestone region may locally permit few surface streams and only occasional ponds. Above Finca Samac was a small water hole dug by an Indian, and in this I secured specimens of *Agalychnis moreletii* and *Rana pipiens*, my only record of those species in the cloud forest. These local populations had entered the habitat from the better-watered Meseta de Cobán below. Similarly, the headwaters of several streams at Finca Chichén have their sources at the base of the cloud forest, and a part of their fauna (that is, *Centrolenella fleischmanni*, *Hyla spinipollex*, *Plectrohyla quecchi*) has the status of entrants from below. It seems obvious, therefore, that were surface waters present to any extent in the cloud forest, its aquatic fauna would probably be much larger.

Many species are dependent not only upon surface water but upon specific types of surface water. At Finca Chichén specimens of *Eleutherodactylus brocchi*, *Hyla spinipollex*, *Plectrohyla quecchi*, and *Rana macroglossa* were abundant in the foaming mountain freshets in regions of high relief. In the quiet parts of those same streams, where they flowed through level pastures, these four species were rare or absent, but *Rana pipiens* occurred abundantly. The presence or absence of the former species could not be attributed to any factor such as temperature or light, for specimens of *Hyla spinipollex* and *Plectrohyla quecchi* at least were taken in a swift mountain stream in an open gorge at Finca los Alpes, some 800 m. lower. Other species are definitely pond inhabitants. In small water holes on the Meseta de Cobán *Hyla baudinii*, *Agalychnis moreletii*, *Rana pipiens*, and *Hypopachus inguinalis*, were, with the exception of *Rana pipiens*, restricted to standing water, while the majority of lowland frogs are pond inhabitants. The aquatic turtles of Alta Verapaz are confined to quiet water, either ponds or sluggish rivers. Apparently unable to cope with the mountain

streams, they have not invaded the highlands, where suitable habitats, especially on the Meseta de Cobán, may be found.

Climate directly and indirectly through its effect upon vegetation appears to be one of the most important of the distributional factors. As previously indicated, on the basis of temperature Alta Verapaz may be partitioned into several vertical temperature belts. Though it cannot be definitely proven, so frequent is the repetition of the break in species ranges at 600 m. and again at 1000 to 1300 m., where features other than temperature appear to be constant, the assumption of temperature as a controlling factor is worthy of consideration. More than 15 per cent of the Alta Verapaz fauna not ascending beyond the 600 m. contour appears to be delimited by temperature. The more conspicuous of such forms are *Anolis h. uniformis*, *Constrictor c. imperator*, *Coniophanes f. fissidens*, and *Bothrops nasutus*. Another 30 per cent of the Quecchian fauna finds its absolute upper limits near 1300 m., which approximates the frost boundary. These are such forms as *Anolis l. bourgeaei*, *Basiliscus vittatus*, *Sceloporus teapensis*, *Drymobius m. margaritiferus*, *Thalerophis m. mexicanus*, and *Bothrops a. asper*. Over 10 per cent of the Alta Verapaz fauna does not descend below 1000 m., where habitats, suitable in apparently every respect except for temperature, occur. Conspicuously absent below that elevation are *Oedipus helmrichi*, *Anolis c. haguei*, *Thamnophis s. fulvus*, and *Adelphicos v. veraepacis*.

Moisture, both as precipitation and as atmospheric humidity, owing to its abundance over most of Alta Verapaz, appears to be a limiting factor in only a single instance, the Cahabón savannas. This enclosed valley supports an impoverished, humid lowland element which is apparently restricted, owing to the less humid conditions existing in the area. The absence of *Bufo valliceps*, likewise not present in the semiarid Río Negro gorge and the interior basins to the south, is particularly striking. Furthermore, restriction of the somewhat less humid Pacific coast *Trimorphodon b. quadruplex* to the Cahabón savannas in Alta Verapaz and the presence of the savanna-inhabiting *Oxybelis fulgidus* in that part of Alta Verapaz alone, suggests the limiting effects of moisture.

In addition to these limiting features of the physical environment, there are unquestionably others. Soils, light, and inorganic cover, for example, cannot be included in this discussion, since studies were not carried on in sufficient detail to give evidence of any distributional effects they might exert upon the fauna.

The effect of biotic features of the environment upon distributional patterns of the herpetofauna are somewhat more difficult to analyze than are the physical features. Vegetation, though often determined by edaphic factors, is primarily dependent upon climate, so that it is often difficult to show that it, rather than some climatic feature of the environment, is the

limiting factor. Nevertheless so closely does the distribution of many forms coincide with floral boundaries that vegetation gives indication of being an important control.

Although the faunas of Finca Samac and Finca Pansamalá possess little in common, environmental conditions except for vegetation are almost the same. The former is a station in the pine forests of the Meseta de Cobán, and the latter lies near the upper limits of the coffee belt (originally broad-leaf forest). At Samac *Oedipus m. mulleri*, *Hypopachus inguinalis*, *Hyla bromeliacia*, and *Sceloporus m. taeniocnemis* were conspicuous items, and all were absent from Pansamalá, where *Sceloporus teapensis*, *Spilotes p. mexicanus*, and *Micrurus a. apiatus* were common; *apiatus* did not occur at either Samac or at any other locality within the pine belt.

The specific limiting features of the cover are varied. In some instances it is the physiognomy of the vegetation. The major factor appears to be the nature of the cover, as savannas, forests, or some special forest type. Such open-country forms as *Sceloporus teapensis*, *Anolis l. bourgeaei*, *Basiliscus vittatus* and *Ameiva u. hartwegi* are strictly savanna inhabitants, whereas *Anolis h. uniformis* and *Ameiva f. edwardsii* are conspicuous forest forms. Neither of these two contrasting groups shows any specificity to any particular local condition within their major environments. The former group, for instance, accepts without partiality true savannas, second growth, and even lightly shaded coffee groves. The latter are found abundantly in all types of lowland forests and may invade heavily shaded coffee or rubber groves where forest-like conditions prevail.

Other species are more specific in their requirements. This is particularly true of the bromeliad community to be discussed later, although it may be moisture requirements or even some reaction such as positive thigmotropism that restricts the community to bromeliads and banana plants.

Some forms appear to be limited less by the grander features of the environment than by some minor factor. Ground litter and humus are requisites for the occurrence of secretive types. A discussion of this habitat will be presented later, but it may be noted here that *Oedipus dofleini*, *Ninia s. sebae*, and *Tantilla schistosa* are typical of the ground-litter community. *Ninia s. sebae* in particular displays direct correlation between its abundance and the amount of ground litter. In relatively clean lowland forest the species occurs sparingly, whereas in the debris of coffee groves and cane fields it is present in great numbers.

Little is known of the interfaunal relationships, so that it is almost impossible to show that there are faunal limitations to distribution. Domestic animals, especially pigs, appear to have a pronounced but local effect. At both Finca Chamá and Finca Cubilguitz, where pigs were permitted to forage around the outbuildings, snakes and lizards, both of which are generally abundant in the edificarian habitat, were noticeably rare.

Aside from this situation other instances of geographic limitations by faunal elements were suggested. For example, *Pliocercus e. salvinii* feeds upon salamanders, as ascertained by stomach examinations. Since the species is a ground form and since no ground salamanders occur above the coffee zone, this fact may account for its absence from the cloud forest.

Although it is improbable that reptilian predators would cause even local extermination of other reptiles and amphibians, local abundance or rarity of certain species may be due to such a relationship. In examining stomach contents of Alta Verapaz snakes, I noted the following prey-predator relationships among the reptiles and amphibians:

PREY	PREDATOR
<i>Oedipus dofleini</i>	<i>Pliocercus e. salvinii</i>
<i>Oedipus helmrichi</i>	<i>Rhadinaea hempsteadae</i>
<i>Oedipus odonnelli</i>	<i>Pliocercus e. salvinii</i>
<i>Oedipus rufescens</i>	<i>Thalerophis m. mexicanus</i>
<i>Hyla bromeliacia</i>	<i>Bothrops n. aurifer</i>
<i>Hyla loquax</i>	<i>Thalerophis m. mexicanus</i>
	<i>Leptodeira a. polysticta</i>
<i>Hyla spinipollex</i>	<i>Thamnophis e. fulvus</i>
<i>Eleutherodactylus bocourti</i>	<i>Thamnophis e. fulvus</i>
<i>Anolis capito</i>	<i>Imantodes l. cenchoa</i>
<i>Anolis h. uniformis</i>	<i>Imantodes l. cenchoa</i>
<i>Sceloporus teapensis</i>	<i>Dryadophis m. laevis</i>
<i>Lygosoma c. cherriei</i>	<i>Scaphiodontophis a. annulatus</i>
	<i>Bothrops a. asper</i>
<i>Pliocercus e. salvinii</i>	<i>Drymarchon s. melanurus</i>
<i>Stenorrhina degenhardtii</i>	<i>Micrurus e. veraepacis</i>

As has been suggested previously, the varied life requirements of the diverse agglomeration of animals which constitute the herpetofauna render the summarization of geographic patterns difficult. The distribution of diurnal terrestrial forms may show a relatively high degree of coincidence, but there is little reason to suspect that patterns characteristic of that group should display any high degree of coincidence with those of nocturnal terrestrial forms. The diurnal forms we might suspect to be limited by maximum and minimum diurnal temperatures and diurnal evaporation indexes, whereas the nocturnal, in contrast, would be restricted by nocturnal conditions.

Assuming that a predominantly lowland group made up of both diurnal and nocturnal species is rendered inactive by temperatures below 15° C., the diurnal species might then find an upper limit of possibly 2000 m., where diurnal temperatures during the coldest month fall to approximately 15° C. Nocturnal species would encounter similar limiting temperatures at night at about 1000 m. elevation. This is a feasible assumption, since there is a mean diurnal variation in temperature of about 3° C. on the Caribbean lowlands of Alta Verapaz, which would indicate no very great

difference in temperature tolerances in the group as a whole. As an observed example, several lotic amphibians find their lower limits at about 800 to 1000 m., a boundary which, to my knowledge, neither coincides with nor even approaches the lower geographic limits of any terrestrial reptile or amphibian.

If varied geographic patterns are thus produced by the major life forms, even more confusion results when a description of the local distribution of any single life group is essayed. The terrestrial herpetofauna of Alta Verapaz includes two very distinct components, the open country or grassland types and the forest types. These two groups, as they extend through the several life belts of the region, have very different geographic patterns. There is, for instance, far greater similarity in the environmental conditions existing in the pastures, natural meadows, and cornfields of the lowlands and of the Meseta de Cobán than there is in the shaded broadleaf forests and open pine parklands, respectively, of the two areas. In response to these similarities and differences, there is a higher degree of relationship between the grasslands communities of the lowlands and Meseta de Cobán than between the forest communities of the two regions.

If summarizing geographic patterns are to be drawn up for the herpetofauna of Alta Verapaz, it would seem that the only feasible approach would be to break down that fauna into its several life forms and consider each independently of the others. In contrasting terrestrials with aquatics, diurnals with nocturnals, or savanna types with forest types, a more accurate but, at this time, confusing picture would result. On the basis of the meager data, it seems best for the moment to essay a few generalizations with the understanding that, when examined in detail, such a general presentation is little more than a working hypothesis for future investigations.

Fortunately the descriptive geographic situation is not quite so hopelessly gloomy. Despite the varied pattern which different combinations of environmental variants produce, there is in Alta Verapaz a fortuitous parallelism in the limits of the several variants.

The windward lowlands are characterized by continually high temperatures, abundant moisture, deep forest or forest-like conditions broken by extensive patches of cleared land approaching savanna conditions, little humus, and quiet streams and ponds. The associated fauna consists of pond amphibians and turtles, a poor humus element, and saurians and ophidians not unlike those known from the savannas and forests of the Petén and British Honduras to the north. In direct contrast to these conditions are those of the Meseta de Cobán, where the temperature is considerably lower, humidity remains relatively high, forests are open pine, humus is abundant especially in coffee groves, streams are swift, and there is little standing water. In response to these conditions the Meseta fauna is quite unlike

that of the lowlands. Turtles are absent, amphibians are predominantly running-water types, a large humus fauna is present, and many of the characteristic saurians and ophidians are Guatemalan plateau derivatives.

Certain physical features transcend several zones, and there is produced some faunal overlap. The characters of the streams of the cloud forest, of the belt of coffee on the mountain slopes, and of the Meseta de Cobán, are almost identical. The aquatic fauna, therefore, of the three regions is much the same, and such species as *Eleutherodactylus brocchi*, *Hyla spinipollex*, and *Plectrohyla quecchi* are common to all. Other physical features vary in the three regions and the entire faunas differ accordingly.

It is fortunate that many reptiles and amphibians possess a remarkably high degree of tolerance to conditions that depart from the optimum. This coupled with often fortuitous coincidence of environmental boundaries in Alta Verapaz enhances geographic generalization.

Thus, through an examination of the environmental factors and the limiting influences they impose upon various species, the geographic patterns of the herpetofauna may be interpreted. It is true that only a fragment of the whole picture is at present visible, yet sufficient data are available to permit an interpretation of the facts along broad and generalized lines.

Nature of the Herpetofauna

Alta Verapaz has been described as the eastern end of the northern Guatemalan mountain arc. It may be likened to an upland peninsula surrounded by a sea of lowlands. Lying in an annectent position between the Caribbean lowlands and the Plateau of Guatemala, and possessing both uplands and lowlands, it is so situated as to have received faunal invasions from both regions. As a result the fauna of Alta Verapaz is made up of several elements characteristic of other faunas in addition to the small group of endemics. Such a situation renders difficult the establishment of the Alta Verapaz assemblage as a distinct fauna.

In the area 129 forms are known to occur (Table I). Considering that such widespread genera as *Xenodon* and *Pseustes* have not been recorded from the region and that at least two unallocated species of tadpoles occur there, the fauna compares favorably in size with that of adjacent regions. More intensive work in the cloud forest, from which only thirty forms are known, should swell the Alta Verapaz species list. It is not improbable that the final count may number about 150 forms. Some 130 have been recorded from the Yucatán lowlands to the north.

In northern Central America, in addition to an ancient and relatively small autochthonous fauna as yet poorly understood, there is an admixture of faunal elements derived more recently from the north and south. These basic elements have combined to produce three basic assemblages in the

TABLE I

A LIST OF THE REPTILES AND AMPHIBIANS OF ALTA VERAPAZ WITH THEIR PROBABLE DISTRIBUTION BY LIFE AREAS

Presence is noted by an X, and an asterisk indicates an Alta Verapaz endemic.

Species	Corozo Life Area	Cahabón Savanna Life Area	Coffee Life Area	Pine Life Area	Cloud Forest Life Area
<i>Gymnopsis oligozona</i>	X		X		
* <i>Oedipus dofleini</i>	X		X		
<i>Oedipus elongatus</i>	X				
* <i>Oedipus helmrichi</i>				X	X
* <i>Oedipus mexicanus mulleri</i>				X	
* <i>Oedipus mexicanus odonnelli</i>			X		X
<i>Oedipus rufescens</i>	X	X	X	X	
<i>Bufo marinus</i>	X	X	X	X	
<i>Bufo valliceps</i>	X		X		
<i>Leptodactylus labialis</i>					
<i>Leptodactylus melanonotus</i>	X				
<i>Eleutherodactylus anzueto</i>					X
* <i>Eleutherodactylus bocourti</i>					X
<i>Eleutherodactylus brocchi</i>				X	X
<i>Eleutherodactylus rhodopis</i>	X				
<i>Eleutherodactylus rugulosus</i>	X		X		
<i>Eleutherodactylus stantoni</i>	X		X		X
* <i>Eleutherodactylus zucanebi</i>				X	X
<i>Centrolenella fleischmanni</i>	X	X	X	X	X
<i>Hyla baudinii</i>	X	X	X	X	X
* <i>Hyla bocourti</i>				X	
<i>Hyla bromeliacea</i>				X	X
<i>Hyla loquax</i>	X				
<i>Hyla picta</i>	X				
<i>Hyla spinipollex</i>			X	X	X
<i>Hyla staufferi</i>	X				
<i>Hyla underwoodi</i>	X				
<i>Agalychnis callidryas</i>	X				
<i>Agalychnis moreletii</i>			X	X	X
* <i>Plectrohyla quecchi</i>			X	X	X
<i>Rana macroglossa</i>			X	X	X
<i>Rana pipiens</i>	X	X	X	X	X
<i>Rana palmipes</i>	X				
* <i>Hypopachus inguinalis</i>				X	
<i>Staurotypus triporcatus</i>	X				
<i>Dermatemys mawii</i>	X				
<i>Chelydra rossignoni</i>	X				
<i>Kinosternon leucostomum</i>	X	X			
<i>Pseudemys scripta ornata</i>	X				
<i>Geoemyda areolata</i>	X	X			
<i>Crocodylus acutus</i>	X				
<i>Crocodylus moreletii</i>	X				
<i>Phyllodactylus lanci</i>	X		X	X	
<i>Thecadactylus rapicaudus</i>	X		X	X	
<i>Sphaerodactylus glaucus</i>	X				
<i>Sphaerodactylus lineolatus</i>	X				
<i>Anolis biporcatus</i>	X		X		
<i>Anolis capito</i>	X		X		
* <i>Anolis cobanensis</i>				X	X

TABLE I (Cont.)

Species	Corozo Life Area	Cahabón Savanna Life Area	Coffee Life Area	Pine Life Area	Cloud Forest Life Area
* <i>Anolis cortezi</i>			X		
* <i>Anolis crassulus haguei</i>					X
<i>Anolis humilis uniformis</i>	X				
<i>Anolis lemurinus bourgeaei</i>	X	X	X		
<i>Anolis limifrons rodriguezi</i>	X	X	X		
* <i>Anolis nannodes</i>			X	X	X
<i>Anolis pentaprion</i>	X				
<i>Anolis petersii</i>				X	
<i>Anolis sericeus</i>	X		X		
<i>Basiliscus vittatus</i>	X	X	X		
<i>Laemactus deborrei</i>	X		X	X	
<i>Corythophanes cristatus</i>	X		X		
<i>Corythophanes percarinatus</i>		X	X	X	
<i>Iguana iguana rhinolopha</i>	X				
<i>Sceloporus malachiticus taeniochermis</i>				X	X
<i>Sceloporus teapensis</i>	X	X	X	X	
<i>Lepidophyma f. flavomaculatum</i>	X		X		
<i>Mabuya m. mabouya</i>	X				
<i>Eumeces sumichrasti</i>	X				
<i>Lygosoma c. cherriei</i>	X		X	X	
<i>Lygosoma incertum</i>				X	
* <i>Ameiva chaitzami</i>		X			
<i>Ameiva festiva edwardsii</i>	X		X		
<i>Ameiva undulata hartwegi</i>	X	X	X		
* <i>Gerrhonotus auritus</i>				X	
<i>Gerrhonotus m. moreletii</i>		X		X	X
<i>Celestus enneagrammus</i>	X				
<i>Xenosaurus rackhami</i>			X		?
<i>Leptotyphlops p. phenops</i>	X		X	X	
<i>Typhlops tenuis</i>	X		X	X	
<i>Constrictor constrictor imperator</i>	X	X			
<i>Scaphiodontophis a. annulatus</i>	X		X	X	
<i>Thamnophis eques fulvus</i>				X	X
<i>Storeria dekayi tropica</i>			X	X	
<i>Dendrophidion vinitor</i>	X				
<i>Drymobius chloroticus</i>	X	X	X	X	X
<i>Drymobius m. margaritifera</i>	X	X	X	X	
* <i>Dryadophis melanolomus laevis</i>	X	X	X	X	
<i>Masticophis m. mentovarius</i>	X	X			
<i>Spilotes pullatus mexicanus</i>	X	X	X		
<i>Drymarchon corais melanurus</i>	X	X	X		
<i>Thalerophis m. mexicanus</i>	X	X	X		
<i>Thalerophis occidentalis praestans</i>	X		X		
<i>Elaphe f. flavirufa</i>	X				
<i>Elaphe triaspis mutabilis</i>	X				
* <i>Lampropeltis triangulum abnorma</i>	X		X	X	
* <i>Pliocercus elapoides salvini</i>	X		X	X	
<i>Pliocercus euryzonus aequalis</i>	X		X	X	
<i>Rhadinaea d. decorata</i>	X				
* <i>Rhadinaea hampsteadae</i>					X
* <i>Rhadinaea veraepacis</i>				X	
<i>Sibon nebulatus</i>	X				
* <i>Tropidodipsas kidderi</i>					X

TABLE I (Cont.)

Species	Corozo Life Area	Cahabón Savanna Life Area	Coffee Life Area	Pine Life Area	Cloud Forest Life Area
<i>Tropidodipsas s. sartorii</i>	X		X		
<i>Ninia diademata</i>	X		X		
* <i>Ninia maculata pavementata</i>	X	X	X	X	X
<i>Ninia s. sebae</i>				X	X
<i>Adelphicos v. veraepacis</i>	X				
<i>Dipsas dimidiatus</i>	X				
<i>Conophis p. pulcher</i>	X				
<i>Coniophanes b. bipunctatus</i>	X				
<i>Coniophanes f. fissidens</i>	X				
<i>Trimorphodon biscutatus quadruplex</i>		X			
<i>Imantodes cenchoa leucomelas</i>	X		X	X	X
<i>Leptodeira annulata polysticta</i>	X				
<i>Oxyrhopus petola aequifasciata</i>	X		X	X	
<i>Oxybelis aeneus auratus</i>	X		X		
<i>Oxybelis fulgidus</i>		X			
* <i>Tantilla bairdi</i>				X	
<i>Tantilla phrenitica</i>	X				
<i>Tantilla schistosa</i>	X		X	X	
<i>Stenorrhina degenhardtii</i>	X		X	X	
<i>Amastridium sapperi</i>	X				
<i>Micrurus affinis apiatus</i>	X	X	X		
* <i>Micrurus elegans veraepacis</i>	X		X	X	
<i>Bothrops atrox asper</i>	X	X	X		
<i>Bothrops godmani</i>					X
<i>Bothrops mexicanus</i>	X		X	X	X
<i>Bothrops nasutus</i>	X				
<i>Bothrops nigroviridis aurifer</i>	X		X	X	X

region, that of the Caribbean lowlands, that of the Pacific lowlands, and a third centered on the highlands. As forms from the Caribbean lowlands of Central America make up the bulk of the Alta Verapaz fauna, this account may be viewed as an analysis of the Caribbean fauna in an upland habitat. Most of the remainder have been drawn from the northern Central American highland fauna, while the Pacific lowlands have contributed only a bare trace.

Endemism in this assemblage amounts to about 20 per cent. This figure is relatively low owing to the fact that a number of widespread Caribbean lowland forms, many restricted to lower elevations, invade the region. Above 1000 m. endemism increases to approximately 35 per cent.

Though many of the following may eventually be discovered in adjacent biotic areas, the majority of the known Alta Verapaz endemics belong to groups sufficiently well known to indicate that they are replaced in other regions by related forms. The twenty-four Alta Verapaz endemics are:

<i>Oedipus dofleini</i>	<i>Anolis c. haguei</i>
<i>Oedipus helmrichi</i>	<i>Anolis nannodes</i>
<i>Oedipus m. mulleri</i>	<i>Ameiva chaitzami</i>
<i>Oedipus m. odonnelli</i>	<i>Dryadophis m. laevis</i>
<i>Eleutherodactylus bocourti</i>	<i>Lampropeltis t. abnormalis</i>
<i>Eleutherodactylus brocchi</i>	<i>Tantilla bairdi</i>
<i>Eleutherodactylus xucanebi</i>	<i>Ninia m. pavimentata</i>
<i>Hyla bocourti</i>	<i>Rhadinaea hempsteadae</i>
<i>Plectrohyla quecchi</i>	<i>Rhadinaea veraepacis</i>
<i>Hypopachus inguinalis</i>	<i>Pliocercus e. salvinii</i>
<i>Anolis cobanensis</i>	<i>Tropidodipsas kidderi</i>
<i>Anolis cortezi</i>	<i>Micrurus e. veraepacis</i>

Upon comparing the fauna of Alta Verapaz with adjacent assemblages, striking differences appear. The fauna of the lowlands of the Yucatán Peninsula to the north, which I have previously named the Petén biotic province (Stuart, 1942, 1943a), resembles the Alta Verapaz assemblage most closely. About 30 per cent of the forms presumably autochthonous to that region (Stuart, 1935; Schmidt, 1941) reached their southern limits in Alta Verapaz or at most extend little beyond the lower Motagua Valley. Some of these species invade the Alta Verapaz uplands. Among the more conspicuous of these forms are:

<i>Oedipus rufescens</i>	<i>Anolis l. bourgaei</i>
<i>Hyla loquax</i>	<i>Anolis l. rodriguezi</i>
<i>Hyla picta</i>	<i>Sceloporus teapensis</i>
<i>Dermatemys mawii</i>	<i>Ameiva f. edwardsii</i>
<i>Geomyda arcolata</i>	<i>Ameiva u. hartwegi</i>
<i>Crocodylus moreletii</i>	<i>Coniophanes b. bipunctatus</i>
<i>Sphaerodactylus glaucus</i>	<i>Coniophanes i. clavatus</i>
<i>Anolis h. uniformis</i>	<i>Tantilla phrenitica</i>

In view of the similarity of certain lowland habitats in the two regions it is difficult to understand why other common northern forms have not invaded Alta Verapaz. Some of the more conspicuous absentees are:

<i>Rhinophrynus dorsalis</i>	<i>Sceloporus chrysostictus</i>
<i>Tripurion petasatus</i>	<i>Cnemidophorus sackii</i> subspecies
<i>Kinosternon acutum</i>	<i>Cnemidophorus d. cozumelae</i>
<i>Anolis tropidonotus</i>	<i>Eumeces schwartzii</i>
<i>Anolis ustus</i>	<i>Leptodeira y. malleisi</i>
<i>Sceloporus l. lundelli</i>	

In addition to the above species, whose absence from Alta Verapaz serves to separate the two assemblages, there are closely allied forms in the two regions. These, generally regional endemics, have obviously been derived one from the other, though the direction of this derivation is not always apparent. Among such species are:

ALTA VERAPAZ FORM	NORTHERN LOWLAND ALLY
<i>Oedipus m. odonnelli</i>	<i>Oedipus m. mexicanus</i>
<i>Oedipus m. mulleri</i>	<i>Oedipus m. mexicanus</i>
<i>Oedipus dofleini</i>	
<i>Eleutherodactylus bocourti</i>	<i>Eleutherodactylus spatulatus</i>
<i>Eleutherodactylus zucanebi</i>	<i>Eleutherodactylus alfredi</i>
<i>Dryadophis m. laevis</i>	<i>Dryadophis m. melanolomus</i>
<i>Lampropeltis t. abnorma</i>	<i>Lampropeltis t. polyzona</i>
<i>Micrurus a. apiatus</i>	<i>Micrurus a. alienus</i>

The zone of transition between the two assemblages is probably broad. On the northern lowlands the fauna boundary may be placed provisionally in an east-west direction at about the latitude of Chisee, where the savannas, so characteristic a feature of the Petén environment, reach their southern limits. Intergrades between the Alta Verapaz *Micrurus a. apiatus* and the Petén *Micrurus a. alienus* from Finca Cubilguitz and reports of the typically more northern *Rhinophrynus dorsalis* no farther south than Chisee certainly suggest this general locale as the boundary.

This northern boundary probably rounds the eastern end of the so-called Sierra de Santa Cruz, an eastward extension of the Pocolhá range, and invades the Yzabal lowlands to the lower Polochic Valley. At Finca Los Alpes on the northern slopes of the Polochic Valley two examples of intergradation between the two assemblages were collected. One was a specimen of *Oedipus m. odonnelli* which bore indications of the middorsal stripe of *Oedipus m. mexicanus*, and the other was a specimen of *Micrurus a. apiatus*, which had narrow yellow bands, indicative of a transition toward *Micrurus a. alienus* (Stuart, 1948).

West of Alta Verapaz a very poorly understood assemblage of species occupies the Sierra de los Cuchumatanes. This fauna shows some relationships to that of the entire upland mass of Chiapas and western Guatemala (Stuart, 1943b: 8) and certain elements have extended their ranges eastward to the highlands of western Alta Verapaz. This fauna, which may characterize a definable biotic area, the Cuchumatán (Stuart: 1942, 1943a), shares the following species with Alta Verapaz:

<i>Eleutherodactylus anzuetoi</i>	<i>Adelphicos v. veraepacis</i>
<i>Sceloporus m. taeniocnemis</i>	<i>Bothrops n. aurifer</i>
<i>Thamnophis e. fulvus</i>	

There are Cuchumatán-Guatemalan Plateau species which do not invade Alta Verapaz. It is understandable that the Temperate zone forms are absent, but as was the case with certain Petén species, it is difficult to explain the absence of others which could find suitable habitats in Alta Verapaz. The genera *Geophis* and *Pituophis* and the species *Bufo bocourti*, the last a dominant in both the Cuchumatán and the Guatemalan Plateau assemblages, may be mentioned as representatives of this group.

Several of the Alta Verapaz forms may have been derived from Cuchumatán stems, though it is more probable that differentiation from a widespread prototypic stock took place independently in the two areas. Forms so related include:

ALTA VERAPAZ FORM	CUCHUMATÁN ALLY
<i>Oedipus helmrichi</i>	<i>Oedipus cuchumatanus</i>
<i>Hypopachus inguinalis</i>	<i>Hypopachus simus</i>
<i>Anolis c. haguei</i>	<i>Anolis c. crassulus</i>
<i>Gerrhonotus m. moreleti</i>	<i>Gerrhonotus m. temporalis</i>
<i>Rhadinaea hempsteadae</i>	<i>Rhadinaea stadelmani</i>
<i>Tropidodipsas kidderi</i>	<i>Tropidodipsas fischeri</i>

Termer (1936:241) takes the Río Copoom as the physical boundary between the Sierra de los Cuchumatanes and the mountains of Alta Verapaz. Though some of the Alta Verapaz forms persist in the eastern Cuchumatán area, it seems probable that the tremendous physical barrier, the gorge of the Río Negro, much of it having the fauna of the dry interior basins, produces a major faunal break.

The faunal assemblage of the dry basins to the south and southwest described by Schmidt and Stuart (1941) is so utterly unlike that of humid Alta Verapaz that there is evidently little relationship between the two. The conspicuous feature of this xeric assemblage is its impoverishment. Published data and unpublished records of several species produce a list of about forty forms. Though the total fauna may possibly be double that figure, many mesic types common in adjacent humid regions are conspicuous by their absence. With reference to Alta Verapaz forms, the salamanders and the anoles are unrepresented in the basins, and the hylas are known from but two wide-ranging species, *Hyla baudinii* and *Hyla staufferi* (Schmidt and Stuart, 1941).

Some genera which might be classed as common xeric species are unknown from Alta Verapaz. Among these *Ctenosaura*, *Cnemidophorus* (two species), *Gymnophthalmus*, and *Crotalus* are most conspicuous.

Several genera common to the two assemblages are represented by different species in most instances unrelated. These include:

ALTA VERAPAZ REPRESENTATIVE	BASIN REPRESENTATIVE
<i>Hypopachus inguinalis</i>	<i>Hypopachus championi</i>
<i>Sceloporus m. taeniocnemis</i>	<i>Sceloporus lunaei</i>
<i>Sceloporus teapensis</i>	<i>Sceloporus v. olloporus</i>
<i>Stenorrhina degenhardtii</i>	<i>Stenorrhina freminwillii</i>
<i>Micrurus a. apaiatus</i>	<i>Micrurus a. hippocrepis</i>

This assemblage of the xeric basins is typical of that of the Zacapan biotic province (Stuart, 1942, 1943a). Its line of contact with that of Alta Verapaz is probably along the band of oak and oak-pine lying between Santa

Rosa and the Salamá basin and along the 1500 m. contour on the northern wall of the Río Negro gorge.

Though known from a bare handful of specimens, it seems likely that a fourth assemblage bounds that of Alta Verapaz on the south and southeast. The mass and age of the Sierra de las Minas is suggestive of faunal distinctness. Like that of Alta Verapaz, its fauna is probably well developed as an assemblage only above about 1000 m., and it may share many species with the adjacent lowlands, particularly those of the Polochic entrenchment. The boundary between this and the Alta Verapaz fauna will probably prove to be the Polochic-Panimá Valley, but since this account is concerned with Alta Verapaz, that valley may arbitrarily be consigned to the Quecchian and the 600 to 1000 m. contour on the northern flanks of the Sierra de las Minas be taken as the faunal boundary. The region occupied by this conjectured fauna to the south was previously named the Sierran biotic province (Stuart, 1942, 1943*a*).

In summation it may be said that the herpetofauna of Alta Verapaz most closely resembles that of the Petén region to the north and east. As will be shown later, it is dominated by an overwhelming number of species which are widespread throughout Caribbean Central America or the northern third of that region. Of these species 40 to 50 per cent are restricted to lower elevations (below about 1000 m. and in most instances below 600 m.). At higher elevations the assemblage shows a considerable amount of faunal similarity to that of the Guatemala highlands lying to the west.

These two groups of species combined with the endemics produce a peculiarly mixed assemblage in Alta Verapaz, which set it off as distinct. The assemblages of adjacent regions are, however, too poorly known to evaluate fully the extent of distinctness of the Alta Verapaz herpetofauna which characterizes the Quecchian faunal area.

Ecology of the Herpetofauna

With the fauna of Alta Verapaz established as an entity characteristic of a definite faunal area, a discussion of the local distribution of the herpetological assemblage within the area may be essayed. First, it will be shown that this Quecchian assemblage may be subdivided into five minor faunal units which occupy as many life areas and, second, an analysis of the several communities within each of the life areas is presented. Certain factors, however, render the attaining of these ends difficult.

First, there is an element which may be defined as the personal error, that is, the lack of uniformity in the study of the several habitats. For example, owing to the fact that coffee fincas on the mountain slopes provide excellent bases from which several vertical zones may be examined, such stations are utilized as frequently as possible. The investigator may devote an equal amount of time to the study of the several altitudinal areas available at any

one finca, but, in addition, it is customary to purchase from Indian workers such specimens as they may encounter. The Indians, for the most part, concentrate their efforts within the coffee zone. Thus, while an investigator is devoting six man-hours during the course of a day's collecting to the cloud forest above the coffee zone, the Indian workers, although securing only incidental specimens, may be devoting several hundred man-hours to the lower belt. As a result, the sixty-five species of reptiles and amphibians secured from the coffee zone in Alta Verapaz, may represent a fairly complete faunal list. From the cloud forest, in contrast, only thirty species are known, a list which is certainly far from complete.

Second, the seasonal activity of the fauna precludes the development of a complete faunal picture. Although each ecological division of Alta Verapaz was studied during both the wet and the dry seasons, the periods of study within those seasons varied greatly from station to station. Wet-season investigations on the northern lowlands were conducted during the first onset of the rains, the period of greatest breeding activity for the amphibians. Wet-season studies of the eastern lowlands were made in September, several months after many of the amphibians had bred and subsequently retired for the year. Obviously, investigations of those two areas were not strictly comparable.

Third, the intense cultivation to which much of Alta Verapaz has been subjected has unquestionably greatly modified zoogeographic patterns, both by restricting the ranges of some species and extending the ranges of others. Though this subject will be treated later, it may be noted here that a number of puzzling faunal enigmas within the coffee zone are undoubtedly due to modifications wrought by human occupation.

Finally, as every geographer well knows, the blocking out of faunal units and faunal zones is based more on actual presence or absence of species than upon relative abundance. Yet, in many instances, the relative abundance is as indicative of faunal similarities or differences as is the presence. Only when one is fully familiar with the habits and habitats of all the species of a region and when one's areal studies are strictly comparable, can an exact estimate of abundance be made. Obviously, I was unable to attain any of these ends, and as a result the crude expression of frequency on an increasing scale of "rare," "moderate," and "abundant" is largely subjective, and at best only an approximation of the actual condition.

In the following description of the distribution of the Alta Verapaz fauna I have taken into account these and other error-producing factors in an effort to present a balanced picture. Many statements will be made which are based less upon empirical data within Alta Verapaz than upon personal experience with the habitats and their communities in adjacent faunal areas. In other instances observations have had to be interpreted with the possibility of the several error-producing factors kept in mind.

It is hoped that more detailed work in the area will substantiate the following descriptions and analysis, which are based for the most part upon observed data with little more than intuition to fill in the enigmatic gaps so often associated with general surveys.

LIFE AREAS OF ALTA VERAPAZ.—The diverse physical and biotic elements of the landscape produce an environmental mosaic which has caused the herpetofauna to become arranged into five distinct assemblages (Map 1). The assemblages occupy five life areas that constitute faunal subdivisions of the Quecchian biotic province which, by its exclusive species or total faunal composition or both, differs from the other subdivisions. Since in its broader outlines vegetation is a manifestation of the combined effects of climate, soils, and topography which in a large measure determine animal distribution, it naturally follows that a high degree of coincidence between floral and faunal boundaries is to be expected, and an analysis of the Quecchian herpetofauna bears out this supposition. It is true that in some instances, the aquatic amphibians for example, this correlation may deviate to some extent, but, as previously noted, the often fortuitous relationship between relief and other environmental factors is sufficiently close that, as a generalization, faunal and floral boundaries are not too widely divergent. But proof of the validity of this contention rests upon a series of analyses which breaks the fauna into decreasingly smaller units.

The basic zoogeographic division of the Alta Verapaz is a lowland-upland arrangement which stems, as shown later, from the sources from which the region's fauna as a whole has been derived. Although the two major assemblages are distinguishable on the basis of origins (lowland or highland), their individuality may best be established through an analysis of presence or absence of genera and species groups, the nature of ecological equivalents (species occupying niches which are roughly comparable in the two areas) in the two faunal groups, and an estimation of abundances in the case of the more tolerant forms. As might be expected no well-marked geographic boundary separates the two units.

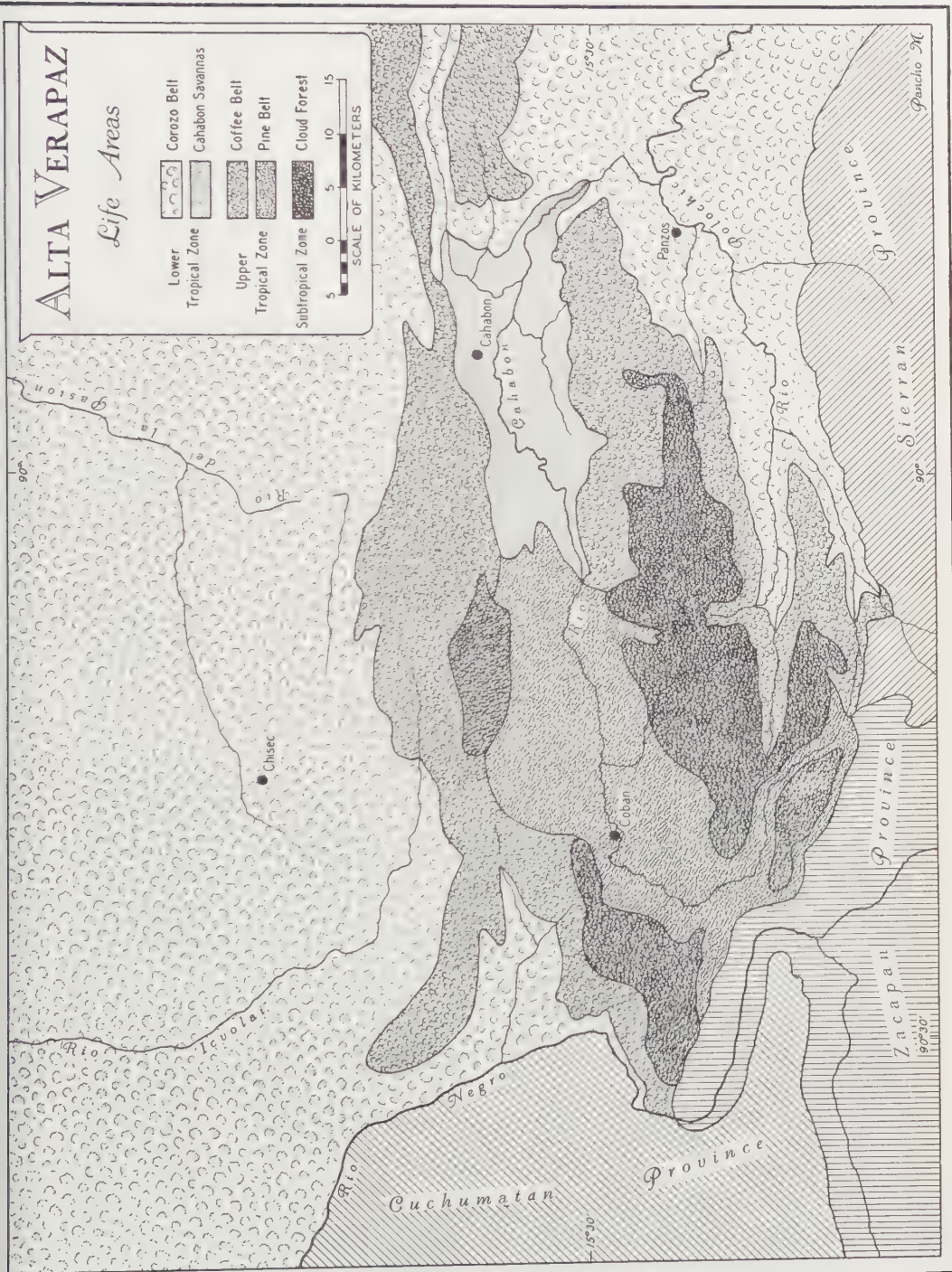
Some of the more conspicuous exclusive groups of the two major assemblages are:

LOWLAND

Leptodactylus
Sphaerodactylus
Basiliscus
Iguana
Ameiva
Constrictor
Drymarchon
Thalerophis
Coniophanes
Testudinata
Crocodylia

UPLAND

Plectrohyla
Hypopachus, inguinalis group
Gerrhonotus
Xenosaurus
Adelphicos, veraepacis group
Rhadinaea, godmani group



MAP 1. The several life areas of Alta Verapaz, based upon Sapper (1901) and observations by Stuart (after Stuart, 1948b).

In addition to these there are less well differentiated forms and species of restricted habitats. For example, the poverty of the lenitic aquatic habitat on the uplands restricts most of the hylids to the lowlands.

Ecological equivalents constitute a sizeable proportion of the species which characterize the two assemblages. Although the exact habitat does not occur on both the uplands and lowlands, roughly similar counterparts of the major habitats are apparent in the two regions. Some striking examples of such ecological equivalents in the forest habitat type of the lowlands and the uplands are:

LOWLAND	UPLAND
<i>Eleutherodactylus rhodopis</i>	<i>Eleutherodactylus anzuetoii</i>
<i>Anolis biporcatus</i>	<i>Anolis petersii</i>
<i>Anolis h. uniformis</i>	<i>Anolis c. haguei</i>
<i>Tantilla phrenitica</i>	<i>Tantilla bairdi</i>
<i>Bothrops nasutus</i>	<i>Bothrops godmani</i>

Despite the difficulty of stating abundance estimates, so obvious is the discrepancy in the relative abundance of some species occurring in both faunal assemblages, that this feature further strengthens the verity of the lowland-upland faunal arrangement. Examples of wide-ranging species displaying unlike abundance in the two regions are:

SPECIES	LOWLAND FREQUENCY	UPLAND FREQUENCY
<i>Oedipus rufescens</i>	rare	abundant
<i>Bufo marinus</i>	abundant	rare
<i>Hyla baudinii</i>	abundant	rare
<i>Sceloporus teapensis</i>	abundant	rare
<i>Ninia s. sebae</i>	rare	abundant
<i>Drymobius chloroticus</i>	rare	abundant
<i>Lampropeltis t. abnormalis</i>	rare	abundant

These two faunal units do not constitute equal proportions of the entire Queechian assemblage. On the basis of our present knowledge of the distribution of the 129 species known from faunal Alta Verapaz, it is indicated that about 75 per cent of the species belong to the lowland assemblage and but 25 per cent to the highland.

As noted previously no sharp boundary demarks the limits of these two faunal units. Many of the species in each community, it is true, are restricted to very low or very high elevations, but there is a broad zone of overlap in which members of the two assemblages occur together. We may, therefore, recognize in Alta Verapaz, three vertical faunal zones, a lowland zone dominated by species of lowland origin, an upland zone in which highland species are most characteristic, and a transition zone supporting an assemblage composed of both highland and lowland species.

The herpetological fauna characterizing the lowland zone contains ninety-seven forms of which all are of lowland origin, though possibly 10 per

cent have differentiated in the Alta Verapaz uplands. An analysis of this assemblage reveals that it is composed of over 40 per cent exclusives. It is, in this respect, the most distinct of the major communities occurring within Alta Verapaz. A second conspicuous feature is its paucity of Quecchian endemics, of which but six (25 per cent of the total Alta Verapaz endemics) form a part of the assemblage and but one is restricted to it. Furthermore, as previously noted, two of these endemics, *Oedipus m. odonnelli* and *Micrurus a. apiatus*, are atypical, revealing characters suggestive of intergradation with annectant forms of the adjacent lowlands. This large and very distinct assemblage constitutes the community of the faunal Lower Tropical zone in Alta Verapaz.

Although there is variation in its limits from locality to locality, the upper boundary of this zone may be placed at about the 600 m. contour. That boundary represents the maximum upper limits of the assemblage and, in the case of exclusives whose distribution appears to be limited by a temperature factor, it may be applicable to Alta Verapaz in its entirety. In other instances where some different distributional factor, as the lenitic environment, is the limiting control, the 100 to 200 m. contour may represent the upper limit. In the Polochic Valley the break between the valley floor and the mountain slopes roughly coincides with the 200 m. contour. Since the aquatic turtles and crocodilians are restricted to lenitic conditions, their upper limit does not exceed 200 m. in that region. On the northern lowlands, on the other hand, the lenitic environment continues up to 400 m. and its community attains higher elevations there than in the Polochic Valley. For the purpose of regional discussion, however, the 600 m. contour may be taken as the absolute upper limit of the Lower Tropical zone.

A small and poorly known assemblage characterizes the highland zone of Alta Verapaz. It includes but thirty forms, of which about 85 per cent are exclusively upland, in either their origin or extant distribution. Although only 20 per cent of the species are restricted to this zone, another 15 per cent transcend its limits to only a very slight extent and may be in part recent invaders into lower elevations. Nine of the twenty-four Quecchian endemics form a part of the community, and four are restricted to it. Perhaps the most striking feature of this assemblage is the manner in which many representatives of the lower zones avoid it. Some thirty-one forms in the Lower Tropical zone range to its lower limits, and but eight transcend that boundary. At least five of these seven are, moreover, so wide-ranging as to be valueless as geographic indicators. The region characterized by this community constitutes the Subtropical zone of Alta Verapaz.

The lower limits of this zone are somewhat more sharply demarked than the upper boundary of the Lower Tropical zone. On the Sierra de Xucaneb it is especially constant and follows the 1300 m. contour with a high degree

of coincidence. The zone is but poorly represented on the other two mountain ranges of the region. On the hills surmounting the Meseta de Cobán the boundary is somewhat less distinct. As a general rule the 1300 m. contour limits the zone, but along streams where broadleaf forest invades the prevalent pine cover of the Meseta, conditions very like those of the Subtropical zone occur as low as 1200 m. The 1300 m. contour, however, proves a serviceable boundary. As previously indicated this contour marks the lower limit of occasional frosts.

Between the assemblages characterizing these two extreme vertical zones of Alta Verapaz there exists a third which is transitional both faunally and environmentally. Of the seventy-nine forms making up this zone's community, about 70 per cent are characteristically lowland forms and about 30 per cent highland forms, almost the same as the proportions for the entire Quecchian fauna. Less than 15 per cent of its members are exclusives, and on this basis it is less distinct than the communities of either the Lower Tropical or Subtropical zones. Eighteen of the twenty-four Quecchian endemics (almost 80 per cent) are present, and seven are exclusives.

The various members of this community of this zone are not uniformly distributed through it with reference to elevation. Some lowland species attain their vertical limits at about 1000 m. elevation; others ascend to 1300 m. Conversely, a few highland species may descend to 800 m., whereas others do not descend below 1000 m. The distribution of some of the more characteristic species of this zone with reference to their vertical limits is shown in Table II.

In occupying an intermediate position between the assemblages of the Lower Tropical and Subtropical zones, the precise relationship of this community is difficult to ascertain. With reference to distance of invasion and degree of abundance, it is indicated that it displays greater resemblance to the assemblage of the former than to that of the latter. Though additional data may disprove this conclusion, for the purpose of a further elaboration of the geography of the Quecchian assemblage, this transitional community is here considered as more closely related to that of the Lower Tropical zone and is hereafter referred to as the Upper Tropical zone. Its limits are provisionally taken as the 600 and 1300 m. contours.

In the foregoing the terms Lower Tropical zone, Upper Tropical zone, and Subtropical zone have been utilized. It should be made clear that these terms have not been used with the life-zone concept in mind. Griscom's (1932) attempt to extend Chapman's (1917) life zones of the northern Andes into Guatemala is a striking example of the fallacy of the life-zone concept as an expression of animal distribution in Guatemala. Schmidt (1936) in his treatment of Guatemalan oedipi, while applying the terminology of Chapman, was obviously not inhibited by the life-zone concept, with the result that he developed a substantial geographic picture. In my

use of life-zone terminology no thought of extralimital extension of the zones is suggested. The whole matter might be clarified were the phrase “a tropical zone” substituted for “the tropical zone.”

Figure 1 presents a summary of the several zonations that have been applied to Guatemala. It may be noted that there is close coincidence between Schmidt’s and my viewpoints. Discrepancy between the two is owing to the fact that Alta Verapaz faces the windward (wet) Caribbean coast, whereas the volcanoes studied by Schmidt face the leeward (drier) Pacific coast. It is well known that all zones on a single mountain mass are lower

TABLE II
VERTICAL DISTRIBUTION OF SOME OF THE MORE CHARACTERISTIC SPECIES OF ALTA VERAPAZ, WHICH REACH THEIR VERTICAL LIMIT WITHIN THE UPPER TROPICAL ZONE (600-1300 m.)

	Species	Below 600 m.	600- 800 m.	800- 1000 m.	1000- 1300 m.	Above 1300 m.
Lowland Species	<i>Eleutherodactylus rugulosus</i>	X	X	X		
	<i>Anolis lemurinus bourgeaei</i>	X	X	X		
	<i>Anolis sericeus</i>	X	X	X		
	<i>Basiliscus vittatus</i>	X	X	X		
	<i>Ameiva festiva edwardsii</i>	X	X	X		
	<i>Ameiva undulata hartwegi</i>	X	X	X		
	<i>Thalerophis m. mexicanus</i>	X	X	X		
	<i>Rhadinaea d. decorata</i>	X	X	X		
	<i>Oedipus rufescens</i>	X	X	X	X	
	<i>Bufo marinus</i>	X	X	X	X	
	<i>Bufo valliceps</i>	X	X	X	X	
	<i>Anolis limifrons rodriguezii</i>	X	X	X	X	
	<i>Sceloporus teapensis</i>	X	X	X	X	
	<i>Drymobius m. margaritiferus</i>	X	X	X	X	
	<i>Spilotes pullatus mexicanus</i>	X	X	X	X	
Highland Species	<i>Tantilla schistosa</i>	X	X	X	X	
	<i>Hyla spinipollex</i>			X	X	X
	<i>Plectrohyla quecchi</i>			X	X	X
	<i>Agalychnis moreletii</i>			X	X	X
	<i>Xenosaurus rackhami</i>				X	?
	<i>Oedipus m. odonnelli</i>				X	X
	<i>Eleutherodactylus brocchi</i>				X	X
	<i>Anolis nannodes</i>				X	X
	<i>Thamnophis sumichrasti fulvus</i>				X	X

on the wetter slopes than on the drier slopes. Griscom’s divergence, which it would seem stems from his attempt to adhere to a concept that utilizes temperature, rainfall, and faunal relations individually in defining the several vertical zones, does not appear to fit the facts. Sapper’s (1932) zones are based upon isothermal limits of dominant plant species, especially crops.

A further analysis of the herpetofauna leads to the establishment of the five communities occupying the five life areas previously referred to. The assemblages of the Lower Tropical and Upper Tropical zones are so distributed as to characterize two communities each. The assemblage of

the Subtropical zone, on the other hand, does not warrant further subdivision on the basis of data now at hand.

Somewhat more than 90 per cent of the Lower Tropical zone may be classified as excessively humid. The remaining less than 10 per cent of that zone, the middle valley of the Río Cahabón, is subhumid. These two habitats, the humid and subhumid lowlands, support two very different herpetological communities. Although there is by no means complete uniformity in the distribution of the fauna of the humid lowlands, the majority of the more characteristic forms are continuous in their distribution. Thus,

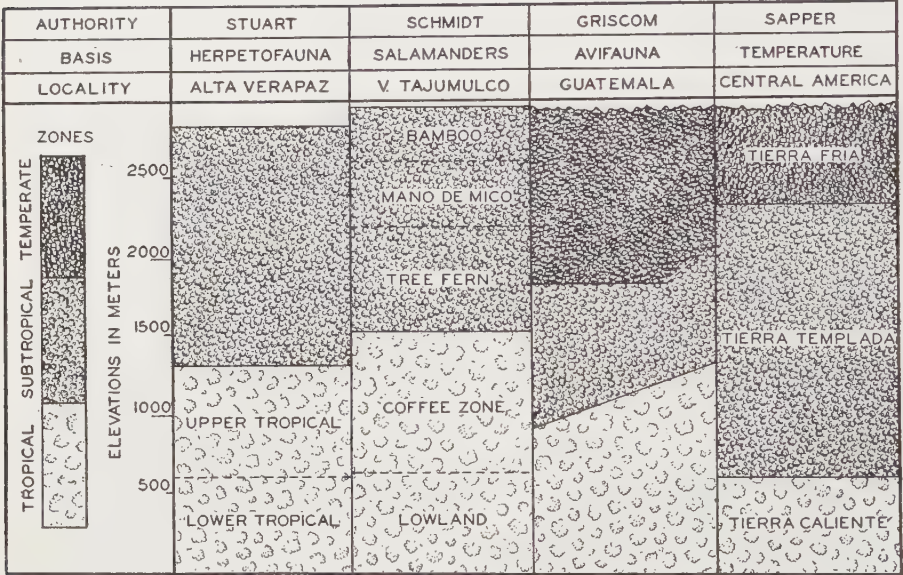


FIG. 1. Diagram of the vertical life belts proposed by various investigators. Note the close coincidence between those of Schmidt (1936) and Stuart. The somewhat lower limits of the belts in Alta Verapaz, as opposed to those of Tajumulco, are probably owing to the higher humidity in that region.

to subdivide further the humid Lower Tropical zone would obscure rather than clarify the geographic picture. If the total assemblage of that habitat is compared with that of the Cahabón Valley, considerable dissimilarity in the two is immediately apparent.

This dissimilarity expresses itself quantitatively rather than qualitatively. The humid lowland fauna numbers ninety-two forms as compared with but twenty-eight in that of the Cahabón Valley. Furthermore, of the forty-three species which do not extend beyond the limits of the Lower Tropical zone in Alta Verapaz, scarcely 10 per cent are common to the two assemblages. It might be concluded from this analysis alone that the Lower Tropical zone and its fauna as previously defined cannot be sustained

as an entity. However, of the twenty-eight forms occupying the Cahabón Valley, only three are not also members of the humid lowland community.

It is obvious, therefore, that the Cahabón Valley community is merely an impoverished assemblage of the more tolerant Lower Tropical zone species. The following in particular are striking examples of characteristic lowland forms which avoid this subhumid habitat:

Bufo valliceps
Agalychnis callidryas
Hyla underwoodi
Anolis biporcatus
Anolis h. unifornis

Anolis sericeus
Ameiva f. edwardsii
Leptodeira a. polysticta
Bothrops nasutus

This assemblage of the Cahabón Valley must not be viewed as but a minor agglomeration, for it is characterized by the presence of three very distinctive species. The peculiar *Ameiva chaitzami* is endemic to it. The xeric or semixerix *Oxybelis fulgidus* is exclusive to the region in the Quecchian area, and *Trimorphodon b. quadruplex*, also a Cahabón Valley exclusive, is the single form of the Pacific coast element which has reached Alta Verapaz.

These two assemblages characterize the two life areas comprising the Lower Tropical zone. The humid part may be designated the Corozo life area and the subhumid, the Cahabón savanna life area.

The two communities which combine to characterize the Upper Tropical zone assemblage are somewhat more distinct than those of the Lower Tropical zone. Their dissimilarity expresses itself primarily qualitatively rather than quantitatively. The habitats occupied by these two communities are the zone of coffee on the three major mountain arcs (600 to 1300 m.) and the pine-covered Meseta de Cobán, which lies above 1000 m. over most of its extent. The somewhat lower extent of the zone of coffee habitat may, in a large measure, be responsible for the slight quantitative difference in the two communities.

Some sixty-one forms have been recorded from the zone of coffee, but only fifty-two can be allocated definitely to the Meseta. Not only are there specific differences in the two communities but there are also some striking discrepancies in the frequency of forms common to the two. Of the seventy-nine forms which comprise the Upper Tropical zone fauna slightly more than 50 per cent are shared by the two communities.

Of the species which are present in the zone of coffee on the mountain ranges at elevations equal to those of the pine zone yet avoiding the pine zone, the following are most conspicuous:

Bufo valliceps
Anolis biporcatus
Anolis l. rodriguezi

Spilotes p. mexicanus
Drymarchon c. melanurus
Micrurus a. apiatus

Similarly, at comparable elevations such species as *Bufo marinus*, *Sceloporus teapensis*, and *Bothrops mexicanus* are more abundant in the zone of coffee than they are upon the Meseta.

Among the characteristic species of the pine zone which do not invade the zone of coffee, the following may be cited:

Hyla bromeliacia
Hypopachus inguinalis
Sceloporus m. taeniocnemis

Thamnophis e. fulvus
Adelphicos v. veraepacis

Among the forms which are more abundant on the Meseta than at similar elevations in the zone of coffee *Agalychnis moreletii*, *Anolis nannodes*, and *Micrurus e. veraepacis* are particularly conspicuous examples.

Although coffee is raised extensively upon the Meseta, it is a far more characteristic feature of the three mountain arms east of that upland. The term Coffee life area is, therefore applied to the mountain slopes lying within the Upper Tropical zone and Pine life area to the Meseta habitat.

As indicated previously the Subtropical zone does not warrant subdivision at this time. It is entirely possible, however, that when more detailed studies can be made on such peaks as Cerro Xucaneb or Cerro Halauté, both in the Sierra de Xucaneb, subdivision of the Subtropical zone may be necessary. Schmidt (1936) was able to distinguish three subzones on the Subtropical zone of the volcanoes of the Pacific slope. The life area of the Subtropical zone of Alta Verapaz will hereafter be referred to as the Cloud Forest life area.

I recognize the following life areas in the Alta Verapaz:

Tropical zone, 1-1300 m.

Lower Tropical zone, 0-600 m.

1. Corozo life area
2. Cahabón savanna life area

Upper Tropical zone, 600-1300 m.

3. Coffee life area
4. Pine life area

Subtropical zone, above 1300 m.

5. Cloud Forest life area

Map 1 presents a generalized scheme of the distribution of the faunal divisions of Alta Verapaz and adjacent regions.

ECOLOGY OF THE LIFE AREAS.—In the nature of the ecological conditions both of the past and of the present lies the key to the composition and origin of the fauna of an area. The nature of the conditions of the past is at best conjecture, but a knowledge of extant habitats and their associated faunas supplies many clues useful to an interpretation of the problems of historical zoogeography. In essaying an explanation of the origin of the

Quecchian herpetofauna it therefore becomes necessary to examine each of the life areas on a topographic scale.

Because one would have to study many localities during both the wet and dry seasons to provide data for a thoroughly finished ecological study of Alta Verapaz, the following account, based upon no such detailed data, is admittedly only a very rough summation of the ecology of the several life areas. For example, Bartlett (1935) has shown that in the Petén to the north there exist eight distinct floral associations within the lowland forest. In my own studies no subdivision of the climax or even subclimax forest of the Corozo life area was considered. The nature of the fauna too has limited the detail of this ecological account. Many tropical species which, superficially at least, show a low population density, have rendered it difficult to allocate with any certainty a number of species to one assemblage or another. This same difficulty has likewise hampered the expression of comparative abundance. I have, therefore, drawn up descriptions of the various habitats and their faunas for the most part upon the basis of material with which I was personally familiar and have allocated to the several assemblages with the assigned statements of abundance only those forms of whose habits I am reasonably certain.

Compared with insects or mammals, herpetological aggregates show little tendency toward multiplication in any one region. Whether herpetologists have been lax in their ecological analyses or whether amphibians and reptiles actually possess a high degree of tolerance to the variable conditions encountered within a single habitat type are questions the answers to which must await more detailed explorations. The fact remains, however, that in northern Central America and probably in many other regions as well, herpetological assemblages are not very closely confined to minor environments within any major habitat.

Within Alta Verapaz only three major habitat types are recognized, the forest, the grassland, and the aquatic-riparian. All three habitat types occur within each of the five life areas. Since the herpetological aggregation of each habitat is drawn from the fauna of the life area in which it occurs, the aggregation of any single habitat type will be different in each life area. To facilitate presentation of the local distribution of the Alta Verapaz herpetofauna, then, one may build an analysis upon the habitat rather than upon the local faunal assemblage.

Although recognizing but three habitat types within Alta Verapaz, it is obvious that there is no uniformity in any single habitat throughout the five life areas. The forest habitat of the pine area is vastly different from the same habitat in the Corozo area. But in presenting conditions of relatively low illumination, comparatively high humidity, vertical layering, and the like, the two forests present similar environmental conditions. They support, as a result, faunal equivalents, which, though often unrelated

genetically, are ecologically similar. In each forest one may find bromeliad inhabitants, leaf-mold types, and scansorial forms. Examples of such ecological equivalents have been listed previously.

The forest habitat type in Alta Verapaz is extremely varied. It includes not only the climax forests but any type of heavy, storied cover which produces climax-like conditions. In the Lower Tropical zone rubber and cacao groves form habitats similar to those of the climax forests and in some instances heavily shaded and often neglected coffee groves of smaller farms may also be included as representatives of the forest habitat. Only occasionally in the coffee area and pine area are coffee groves sufficiently shaded to produce forest-like conditions.

Occasionally, this inclusion of cultivated land in the forest habitat produces peculiar anomalies. One such instance is the case of the cacao groves of the Cahabón savannas. On the pine savannas broadleaf forest occurs only as a very narrow belt along the larger streams, but the cacao groves give rise to a humid, broadleaf-forest habitat where one probably never existed prior to human occupancy.

The forest habitat type may be characterized as presenting storied distribution of minor habitats (ground surface, elevated bromeliads, forest roof, etc.), low illumination beneath the forest canopy, high humidity with low evaporation, low ground temperature, generally an absence of dense ground cover (occasionally abundant in the pine area), some protection against high winds and torrential rains, and continuity in temporal extent.

Like the forest habitat type, the grassland habitat is represented by extremely varied cover types. To what extent the grassland habitat type occurred in Alta Verapaz prior to human occupancy, can only be conjectured. There is reason to believe that the Cahabón savannas are natural, but it is doubtful if such cover originally occurred to any great extent elsewhere in the region. As an extensive environment savannas extend no farther south than Chisec from the north on the Yucatán Peninsula. Open cover occurred to the east only as pine and local grassland areas through southern British Honduras and in the lower Yzabal embayment. This pine of the lowlands, with light undergrowth, provides a habitat unlike that of the heavily undergrown pine of the Meseta de Cobán. It presents conditions more or less typical of the grassland habitat type.

The grassland habitat type following the destruction of the forest was unquestionably a natural phenomenon in the region prior to human occupancy. Both fire and occasional extensive inundations in abnormally wet years must have caused the destruction of considerable tracts of climax forest. Since human occupancy this destruction of the forest has probably been extended.

The most extensive grassland habitat type in Alta Verapaz is the low second growth of abandoned milpas. When typically developed, the sec-

ond growth proper, depending upon age, ranges from a dense cover of herbaceous plants, through an older rank tangle of small trees, shrubs, and undergrowth, to the subclimax forest. This last, as previously indicated, is included in the forest habitat. Cultivated land of several types is also included in the grassland habitat type. Permanent pastures, cornfields, and lightly shaded coffee groves present ecological conditions similar to those of true savannas.

As opposed to the forest habitat, vertical distribution of minor habitats is a less conspicuous feature of the grassland habitat type. Owing to the absence of a heavy canopy, illumination is here higher, while ground temperatures and evaporation are probably similarly increased. Cover of all types is more abundant than in the forest, but that cover offers less protection against the elements than does the canopy of the forest. Another distinctive feature of this habitat, as it probably occurred naturally in Alta Verapaz, is its lack of continuity, occasionally areally and generally temporally as well. In the majority of instances, it remains a habitat surrounded by forest. Thus, the forest serves as a barrier separating the often isolated patches of the grasslands habitat type. Furthermore, the grassland habitat is generally short-lived. Natural savannas are about as permanent as the forest, but pastures, cornfields, and coffee plantations do not exist long. A single coffee grove is generally not maintained more than fifty years, after which replanting is necessary. In the case of agricultural lands other than coffee groves, burning is often an annual measure as an aid in clearing.

These factors all combine to produce extreme variability in the grassland fauna. Only the more tolerant species are able to transcend the often extensive forest barrier between grassland-like habitats. The often ephemeral nature of the habitat generally precludes the possibility of climax development of the grassland fauna. Frequent firing similarly retards establishment of many species in such a region, and even upon natural savannas, which are particularly susceptible to fire, a faunal equilibrium is probably rarely attained. As a result the grassland assemblage varies from locality to locality and the nature of its climax composition is at best a conjecture.

The aquatic-riparian habitat includes two subdivisions, the lenitic habitat and the lotic habitat. Generally speaking, the lenitic is characteristic of the Lower Tropical zone and the lotic predominantly of the Upper Tropical and Subtropical zones. Unlike the two habitats described above, the aquatic-riparian habitat represents a vein running through the matrix of the forest or second-growth habitats. As such the character of its fauna is more often determined by its location with reference to surrounding habitats than by its physical conditions. This is especially true of terrestrial forms, particularly snakes; these visit the habitat to feed upon frogs in their breeding season. Furthermore, in response to the pronounced

seasonal precipitation in Alta Verapaz, the assemblage of this habitat is varied in its annual composition. This is especially true of the lenitic environment. In the dry season ponds may shrink to mere mud holes or even become completely dry; the more aquatic animals are sparse or absent and the terrestrial visitants avoid the habitat. During the wet season, on the other hand, the reverse condition renders this habitat the most heavily populated of all habitats, both with reference to species and to individuals.

Although drawing heavily for its fauna on that of the surrounding habitat type, the aquatic-riparian habitat certainly supports a distinct assemblage of its own. Here may be included not only the aquatic turtles and amphibians, but a number of reptiles which are always associated with riparian conditions. Among the more conspicuous examples of the latter group may be mentioned the two crocodiles (*Crocodylus*) of Alta Verapaz and *Iguana i. rhinolopha*.

Two minor habitat types, the bromeliad-banana and the leaf mold, will be treated independently. Although these minor habitats are present in all the life areas, and like the aquatic-riparian habitat, are woven into both the forest and grasslands, their associated faunas are in many instances so specialized that a statement of their distributions according to life areas would obscure rather than clarify their ecology. The two habitats will be characterized later.

Many authors have included in their ecological descriptions discussions of the edificarian habitat. In Alta Verapaz this habitat, in providing cover, abundance of food (insects around refuse, grain for mammals upon which larger snakes feed), and similar features, supports a varied fauna of which several species occur with far greater frequency than under more natural conditions. Nevertheless, the habitat does not appear to have exercised any more than a very local geographic effect upon the Quecchian assemblage as a whole. Since it has apparently not been active in determining either the composition or present distribution of the herpetofauna of even a single life belt, in the following discussion it will not be considered as a separate entity.

In support of the inconsistent ecological treatment outlined above, it may be reiterated that the elaboration of that outline does not constitute an end *per se*. It is meant to serve, rather, as the basic data upon which an interpretation of the composition and origin of the Quecchian herpetofauna rests. Throughout the following discussion similarities rather than differences in ecosystems must be stressed, since it is in the nature of extant habitats and their communities and the similarities they possess one to the other locally as well as to extralimital ecosystems that an explanation of the presence or absence of various forms is to be found and the lines of dispersal of faunal elements are in a large measure to be traced.

The Corozo life area makes up 65 per cent of the Quecchian faunal area.

Its lower boundary is that of the Queechian area on the west, north, and east. From the east, the upper boundary extends up the Polochic Valley and its tributaries to 600 m. elevation on the valley slopes (excepting the Cahabón Valley), doubles back around the Sierra de Santa Cruz, an eastern extension of the Pocolhá range, and then continues westward along the 600 m. contour on the north slope of the Sierra de Pocolhá to join the western boundary of the Queechian (Río Negro).

Studies of this life area were made at four localities, Chamá in the west (wet and dry season), Samanzana and Cubilguitz in the north (wet season only), and Panzós in the east (wet and dry season). Other major collections from the belt include those of Godman and Salvin from "Verapaz, low forest," probably the Cubilguitz area in 1861; of Bocourt from Panzós in 1865; of the United States Department of Agriculture in the Polochic Valley, between 1902 and 1914; and of Anthony at various localities between 1925 and 1928 (Stuart, 1948a).

Although many environmental features of the corozo area are duplicated in other life areas, those particularly characteristic of the area are: low relief except locally in the north; high temperatures with but slight diurnal and annual range; abundant precipitation; widespread distribution of the lotic habitat; and continuity of forest habitat type as opposed to discontinuity of the grasslands habitat type.

A total of ninety-two forms is definitely known or suspected to be present in this life area. This includes twenty amphibians, two crocodilians, six testudines, twenty-three saurians, and forty-one ophidians. Only five Queechian endemics enter the area and none of these is exclusive to it. Some thirty-five forms are exclusive to the corozo area in the Queechian faunal area.

Of the several life areas in Alta Verapaz, the corozo belt displays the greatest variation in physical features. The northern section has greater relief, is more humid, and is poorer in the grassland habitat type, especially cultivated land, than the eastern section. In the north a series of east-west ridges, decreasing in height northward, produces moderate relief (Pl. I, Fig. 1). At Chamá these ridges rise some 450 m. above the valleys, whereas at Samanzana they do not exceed 100 m. Between the ridges lie low, often poorly drained valleys of widths up to possibly five miles, which are broken by irregularly placed low hills. Where streams and rivers cut through the ridges, rapids are so violent as to prevent navigation. In the intervening depressions running water approaches lotic conditions and ponds and swamps are numerous. Agriculture and its associated grassland habitat type is practically restricted to the valleys (Pl. II, Fig. 2), but is at best scattered and discontinuous. The forest habitat type occupies the ridges almost completely and, especially towards the north, is often continuous across the intervening valleys.

In contrast with this situation the eastern part of the corozo area forms a part of the Yzabal embayment and is largely a level plain (Pl. I, Fig. 2). Only where the lower slopes of the mountains contact the lowlands is there more than low relief. As a result, even the rivers present lotic-like conditions. Though precipitation is high, it is considerably less than in the north. Furthermore, annual inundation by the Río Polochic (Pl. III, Fig. 2) and somewhat more extensive clearing than exists in the north have greatly extended the grassland habitat type.

These differences in the environment are expressed in the composition of the herpetological assemblages of the two regions. In the north the grasslands fauna is more poorly developed than it is in the east. This is particularly evident in the absence of *Geoemyda areolata*, *Anolis c. rodriquezii*, *Sceloporus teapensis*, and *Ameiva u. hartwegi* from the former. Conversely, deep-forest forms such as *Anolis h. uniformis*, *Ameiva f. edwardsii*, and *Bothrops nasutus* are infrequent in the east. Apparently unable to negotiate rapids, *Chelydra rossignonii* and *Pseudemys s. ornata* are not members of the aquatic fauna in the north. Despite these and other faunal differences in the two parts of the corozo belt, there is, as previously indicated, sufficient similarity between the two to preclude any possibility of elevating them to the status of separate life areas.

The forest habitat type, where typically developed, does not appear to support a large fauna. Though inundation, especially in the Polochic Valley, undoubtedly inhibits the development of large populations, it is possible that the paucity of species and individuals in the forest fauna is not an actuality. The low illumination within the forest and the sombre hues of its associated faunal assemblage render collecting difficult. Where an opening in the forest roof increases illumination on the floor, reptilian life becomes more conspicuous. It is entirely possible, moreover, that such openings produced by trails or windfalls attract individuals from the deeper shade. Certainly such localities enhance collecting fortune. Furthermore, it is entirely possible that some forms found in the grasslands habitat type along the forest margin are more typical of the forest than of more open country.

In Alta Verapaz forest-like conditions are inevitably indicated by the presence of *Ameiva f. edwardsii* and *Anolis h. uniformis*. This habitat supports the following characteristic species. Only species personally collected or observed are recorded. A dagger denotes a form probably restricted to an assemblage in the life area under discussion:

- † *Eleutherodactylus rhodopis* (rare)
- † *Anolis h. uniformis* (abundant)
- † *Ameiva f. edwardsii* (abundant)
- † *Thalerophis o. praestans* (rare)

- † *Pliocercus e. salvinii* (rare)
- † *Tropidodipsas s. sartorii* (moderate)
- † *Coniophanes f. fissidens* (moderate)
- † *Bothrops nasutus* (moderate)

In addition, *Eleutherodactylus rugulosus* (rare) and *Ninia s. sebae* (rare) were noted as members of the fauna, but it is uncertain whether or not they are restricted to this environment in the corozo area.

The grasslands habitat type with its tremendously varied conditions, ranging from open grasslands to rank brushland, yielded a fauna of three times as many species as were observed in the forest habitat type. Since the Corozo life area of Alta Verapaz probably supported few or no natural grasslands south of Chisee in pre-Indian times, the presence of a large grasslands fauna in the region is a rather anomalous condition. This same situation was also observed in the coffee area, which was apparently unbroken forest land before the coming of man. This anomaly will be considered later.

It may be noted, however, that numbers of species observed only in the grasslands habitat type are, more probably, forest forms of a relatively high tolerance which, though unable to invade the grasslands proper, can survive in dense *monte*. In the open grasslands habitat type they are more conspicuous than in the forest, so that such forms although primarily forest species, were observed only in the grasslands habitat type. Among such species may be listed *Anolis capito*, *Laemactus deborrei*, and *Micrurus a. apiatus*.

The extremes of the grasslands habitat type, represented by pastures and brushlands approximating forest conditions, yielded few specimens. The pastures possibly do not provide sufficient cover and collecting in the brushlands is such a noisy undertaking that the fauna retreats before being encountered (Pl. II, Fig. 1). Cornfields, lightly shaded coffee groves, and recently abandoned agricultural plots provide the optimum conditions both for fauna and collection in this habitat.

A rather interesting feature of the grasslands is the frequent occurrence of scansorial species (*s. l.*). This is not an exclusive feature of the fauna in the Quecchian, but pertains as well to the fauna of the Petén grasslands and to that of the dry, outer end of the Yucatán Peninsula. True arboreal types are absent, but forms such as *Anolis sericeus*, *Thalerophis m. mexicanus*, and *Leptodeira a. polysticta* are more frequent among the branches of low bushes and scrubby trees than they are on the ground.

The most characteristic species of the grasslands fauna proved to be *Sceloporus teapensis* and *Ameiva u. hartwegi* in the east and *Anolis sericeus* in the west. The diversity in the local abundance of these species which are so characteristic of the grasslands of the entire Yucatán Peninsula, accentuates the differences in the grasslands fauna of the eastern and western portions of the Quecchian, to which reference has already been made. To this fauna can be definitely allocated the following:

<i>Kinosternon leucostomum</i> (moderate)	† <i>Constrictor c. imperator</i> (moderate)
† <i>Anolis l. bourgeaei</i> (moderate)	<i>Dryadophis m. laevis</i> (moderate)
† <i>Anolis l. rodriguezii</i> (rare)	† <i>Drymarchon c. melanurus</i>
† <i>Anolis sericeus</i> (abundant)	† <i>Thalerophis m. mexicanus</i> (moderate)
<i>Basiliscus vittatus</i> (abundant)	<i>Lampropeltis t. abnormalis</i> (rare)
† <i>Sceloporus teapensis</i> (abundant)	<i>Bothrops a. asper</i> (moderate)
† <i>Ameiva u. hartwegi</i> (abundant)	

In addition to the above, other species were observed in the grasslands habitat type, but they occurred so sparingly in some instances that it cannot be said with certainty whether they are permanent members of the assemblage or merely transients. Some, like the bufos, are seasonal members. This group includes:

<i>Bufo marinus</i> (abundant)	<i>Eumeces sumichrasti</i> (moderate)
<i>Bufo valliceps</i> (abundant)	<i>Drymobius m. margaritiferus</i> (moderate)
<i>Sphaerodactylus lineolatus</i> (rare)	<i>Spilotes p. mexicanus</i> (rare)
<i>Anolis biporcatus</i> (rare)	<i>Imantodes c. leucomelas</i> (rare)
<i>Anolis capito</i> (rare)	<i>Leptodeira a. polysticta</i> (rare)
<i>Laemactes deborrei</i> (rare)	<i>Micrurus a. apiatus</i> (rare)
<i>Mabuya m. mabouya</i> (rare)	

Owing to its distribution throughout both the preceding habitat types in addition to its varied physical nature and seasonal modifications, the aquatic-riparian habitat is the most complex of all environments in Alta Verapaz.

Although the lotic environment is well represented in the corozo belt, it is neither so widespread nor so conspicuous a feature of the life area as the lenitic habitat. Its associated community is, moreover, only poorly developed. Furthermore, much of the lotic environment, though strictly running water, presents conditions which, insofar as many aquatics are concerned, are more of the lenitic type.

The lotic community is especially poorly developed in the north. As previously suggested, the rapids which punctuate the streams at intervals have apparently proven too great a barrier to the upstream movement of many species. Only two species, *Centrolenella fleischmanni* and *Rana palmipes*, may be said to be tolerant to the typical lotic environment. In running water which is relatively quiet, the following as well may be found:

<i>Bufo marinus</i> (rare)	<i>Kinosternon leucostomum</i> (moderate)
<i>Rana pipiens</i> (rare)	<i>Pseudemys s. ornata</i> (rare)
<i>Dermatemys mawii</i> (moderate)	<i>Crocodylus acutus</i> (abundant)
<i>Chelydra rossignoni</i> (rare)	

The lenitic community in Alta Verapaz, on the other hand, reaches its maximum development within the corozo area. In the north the depressions separating the ridges contain numerous shallow ponds, some seasonal and others permanent, while in the east vegetation-choked oxbow lakes on the Polochic flood plain are numerous. Only one lake of any size occurs on the

lowlands, the great swamplike Laguna del Zarco which, though visited, yielded little faunal data.

Apparently the availability of suitable habitat has little effect upon the seasonal rhythm of the greater portion of the aquatic community, especially the amphibians. During the dry season the aquatic assemblage, with the exception of such widely distributed, perennially active forms as *Bufo marinus* and *Rana pipiens*, is no more in evidence in permanent ponds than in the dry bottoms of seasonal water holes. With the breaking of the heavy rains, generally about mid-May, the aquatic fauna becomes active. Maximum activity is attained during the first few weeks of the wet season, following which the majority of the species are represented by only an occasionally active individual. Little difference in the fauna of the permanent and seasonal ponds at any one locality was observed. Only the more aquatic turtles and crocodilians, *Dematemys* and *Pseudemys* especially, did not appear in the seasonal ponds during the wet season.

In displaying geographic continuity in any single locality, the lotic habitat differs greatly from the lenitic which is discontinuous in its distribution. As a result of the continuity of the lotic habitat, the associated fauna is relatively uniform despite variation in adjacent habitat and community types. Thus, although a stream's course may extend through both the forest and grassland habitat types, its amphibian community remains unvaried. Lenitic communities, however, show some modification depending upon the locale of the habitat. At Chamá, for instance, woodland ponds supported *Hyla loquax* and *Agalychnis callidryas* in addition to the amphibians characteristic of ponds in the grassland habitat type. *Kinosternon leucostomum*, however, which is fairly abundant in pools in the second-growth habitat type, was never found in pools within the forest.

The riparian habitat is frequented not only by true aquatics (those necessarily aquatic during at least one stage of their life cycle) but also by species seeking some special environmental feature of the habitat, a moist substratum for example, and by forms which may be classed as visitants. Of these *Basiliscus vittatus* and *Drymobius m. margaritifera* are conspicuous members of the community for undetermined reasons. *Iguana i. rhinalopha* frequents sandy river banks apparently because they offer suitable conditions for egg deposition. The nocturnal *Leptodeira a. polysticta* is unquestionably a wet-season visitant invading the habitat to feed upon the frog population, which is largely nocturnal in its breeding habits. Taylor and Smith (1945:600) found this species gorging on the eggs of *Agalychnis moreletii*, which were suspended above the water from overhanging branches.

The following species make up the aquatic-riparian assemblage (expressions of abundance are based upon conditions during the first half of the rainy season):

<i>Bufo marinus</i> (abundant)	† <i>Rana pipiens</i> (rare)
<i>Bufo valliceps</i> (abundant)	† <i>Dermatemys mawii</i> (rare)
† <i>Leptodactylus labialis</i> (abundant)	† <i>Chelydra rossignonii</i> (rare)
† <i>Leptodactylus melanontus</i> (abundant)	<i>Kinosternon leuocostomum</i> (abundant)
† <i>Centrolenella fleischmanni</i> (moderate)	† <i>Pseudemys s. ornata</i> (moderate)
† <i>Hyla baudinii</i> (abundant)	† <i>Crocodylus acutus</i> (abundant)
† <i>Hyla loquax</i> (abundant)	<i>Basiliscus vittatus</i> (abundant)
† <i>Hyla picta</i> (abundant)	† <i>Iguana i. rhinolopha</i> (moderate)
† <i>Hyla staufferi</i> (rare)	<i>Drymobius m. margaritiferus</i> (rare)
† <i>Hyla underwoodi</i> (abundant)	† <i>Coniophanes b. bipunctatus</i> (rare)
† <i>Agalychnis callidryas</i> (abundant)	<i>Leptodeira a. polysticta</i> (rare)
† <i>Rana palmipes</i> (rare)	

The Cahabón Savanna life area comprises but 4 per cent of the area of the Queechian. It occupies the rift valley drained by the lower course of the Río Cahabón between Taquincó and the level of Finca Xicacao. As a mean, its boundaries are represented by the 600 m. contour on the surrounding mountain slopes, but to the west, where it is in contact with the pine belt, it may ascend to as high as about 1000 m. Unlike the corozo area, the Cahabón savannas are a small compact unit displaying a high degree of physical uniformity throughout their extent.

Studies were made at but two localities, fincas Canihor and Los Pinales, both of which are near the geographic center of the area. The few specimens collected by travelers during the late 1800's do not materially enhance the data secured in my own collecting.

The environmental characteristics of this life area include moderate to high relief, high temperatures, relatively little precipitation though often high atmospheric humidity, lenitic habitat poorly developed, and almost complete absence of the forest habitat type.

Only twenty-eight forms have been recorded from the Cahabón savannas. They are represented by five amphibians, two turtles, eight lizards, and thirteen snakes. Only two Queechian endemics, one exclusive to the area, are known to occur there, and but three species are restricted to this life area within Alta Verapaz.

The natural forest habitat type (Pl. V, Fig. 1) within this enclosed valley is restricted to a very narrow belt, never more than a few meters in width, of open broadleaf forest along the major water courses (gallery forest) and to scattered groves of pine with moderate undergrowth. Owing to the scant precipitation the scattered coffee and cacao groves are heavily shaded and produce dry-forest conditions. Despite the occurrence of two forest types in the region, it is doubtful that a distinct forest assemblage was ever well developed even in the broadleaf forest. Although there is continuity of the eastern forest of the corozo area into the valley along the Río Cahabón, the indicators of the forest fauna of that area, *Ameiva f. edwardsii* and *Anolis h. uniformis*, are absent. At best the natural forest habitat type is

but weakly developed and represents merely an extreme grassland habitat type. With the possible exception of *Oedipus rufescens*, the composition of the forest fauna suggests that it is an assemblage of the shade-tolerant, grassland-community species.

The following were secured in wooded groves:

<i>Oedipus rufescens</i> (rare)	<i>Ameiva u. hartwegi</i> (abundant)
<i>Bufo marinus</i> (abundant)	<i>Dryadophis m. laevis</i> (moderate)
<i>Anolis l. bourgeaei</i> (rare)	<i>Ninia s. sebae</i> (rare)
<i>Basiliscus vittatus</i> (abundant)	<i>Micrurus a. apiatus</i> (rare)
<i>Sceloporus teapensis</i> (abundant)	

The grassland habitat covers possibly 95 per cent of the Cahabón Savanna life area. The greater part of the region supports a true savanna cover of tall grasses with scattered pines and low broadleaf trees (Pl. V, Fig. 2). Cultivated fields are not unlike those of the corozo area, but second growth following abandonment of such plots, while dense, never approaches in elevation the second growth of the corozo area. A final feature producing a great environmental difference between this habitat type in the corozo area and that of the Cahabón savannas is fire. In the savanna area, owing to the nature of the cover, fire is both more widespread and possibly more destructive than in the former.

It has been suggested by certain botanists (*in litt.*) that this factor may cause persistence of savannas which might otherwise develop a forest cover. The herpetofauna does not support the contention. The presence of the endemic *Ameiva chaitzami* and the occurrence of the true savanna indicators *Trimorphodon b. quadruplex* and *Oxybelis fulgidus* in only this life area in Alta Verapaz are strongly suggestive of the climax nature of these savannas.

Throughout the grassland habitat type the associated fauna is relatively uniformly distributed despite local differences in floral features. The assemblage is composed of the following forms:

<i>Bufo marinus</i> (abundant)	<i>Ameiva u. hartwegi</i> (abundant)
† <i>Geoemyda areolata</i> (rare)	† <i>Constrictor c. imperator</i> (rare)
<i>Anolis l. bourgeaei</i> (abundant)	<i>Dryadophis m. laevis</i> (rare)
† <i>Anolis l. rodriguezii</i> (rare)	† <i>Spilotes p. mexicanus</i> (rare)
<i>Basiliscus vittatus</i> (abundant)	† <i>Drymarchon c. melanurus</i> (rare)
<i>Sceloporus teapensis</i> (abundant)	† <i>Oxybelis fulgidus</i> (rare)
† <i>Ameiva chaitzami</i> (moderate)	† <i>Bothrops a. asper</i> (rare)

The aquatic-riparian fauna is poorer in the Cahabón savannas than in any life area in Alta Verapaz. The true lenitic habitat, owing to the relief, is almost nonexistent in the region, and the assemblage associated with it is, therefore, restricted to pools in the streams. Over most of the area lotic conditions prevail in the aquatic habitat. This factor combined with sub-humid conditions greatly restricts the aquatic-riparian fauna. This assemblage includes:

<i>Bufo marinus</i> (abundant)	<i>Basiliscus vittatus</i> (abundant)
† <i>Centrolenella fleischmanni</i> (moderate)	<i>Ameiva u. hartwegi</i>
† <i>Hyla baudinii</i> (abundant)	

Though the Coffee life area should legitimately be discussed at this point, its transitional nature renders it difficult of description until annectent life areas have been treated. An analysis of the area will, therefore, be delayed until the pine and cloud forest life areas have been examined.

The Pine life area comprising approximately 7 per cent of the Queechian faunal area is, from the standpoint of its communities, the most difficult of the several life areas to interpret. It is confined to the Meseta de Cobán and ranges from 1000 m. to 1300 m. in elevation. Although pine and oak forests represent the "dominant" vegetation type on the Meseta de Cobán, the pine area fauna is composed of species most of which are restricted to the broad-leaf vegetation type. Several interpretations of this anomaly, none of them particularly satisfactory, will be suggested, but it is believed that a full understanding of the fauna of the area will be delayed until more complete studies can be made of the extensive pine-covered plateau and mountains to the west.

I carried on studies in the pine area at Finca Samac and Finca Chichén. Mr. K. P. Schmidt secured material for the Chicago Natural History Museum from the former locality and from Cobán. A considerable number of scattered collections are preserved in various museums with Cobán given as the locality for the majority of the specimens, but many records from that locality are questionable since, in many instances, the town served merely as a shipping point (Stuart, 1948a: 91-92).

As a habitat the pine area is one of moderate elevation, high relief, moderate temperatures, and relatively high precipitation. It supports the maximum faunal development of the lotic habitat in Alta Verapaz.

From the pine area fifty-two species have been recorded. They include sixteen amphibians, thirteen lizards, and twenty-three snakes. Sixteen of the Alta Verapaz endemics occur within the area and nine forms are exclusive to it.

The most extensive vegetation cover of the forest habitat type is pine. In these forests, in which undergrowth is often heavy (Pl. VIII, Fig. 1), both oak and liquidamber are conspicuous features. The fauna of this habitat is extremely poor both in number of forms and in their abundance. Just what group of factors is responsible for this situation is unknown, but it is suggested that the pine forest possesses all the disadvantages of a broadleaf forest habitat type with none of its normally present advantages. Thus ground temperatures and illumination are rather low, distinctly disadvantageous features of forests in general. Contrasted with the advantageous feature of the broadleaf forest in the same region, the pine forest lacks a humus layer, the bromeliad habitat is poorly developed, evaporation is com-

paratively higher because of the more open forest roof, and ground moisture is probably lower, owing to absence of humus, shallow soils, and greater evaporation. These latter features are especially disadvantageous to the amphibians.

In the pine forest I secured the following assemblage:

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|--|--------------------------------------|
| † <i>Anolis petersii</i> (rare) | † <i>Rhadinaea veraepacis</i> (rare) |
| <i>Sceloporus m. taeniocnemis</i> (abundant) | |

In the broadleaf forest along streams and similarly humid situations—valleys as compared with hillocks—and in coffee groves a large fauna exists. As a considerable part of the broadleaf forest habitat borders streams, it is difficult to single out those species which may be aquatic-riparian types rather than forest forms. The great majority of the species in the broadleaf forest habitat type are either bromeliad or ground-litter inhabitants. This assemblage includes:

- | | |
|--|--|
| † <i>Oedipus helmrichi</i> (abundant) | † <i>Anolis nannodes</i> (moderate) |
| † <i>Oedipus m. mulleri</i> (moderate) | <i>Sceloporus m. taeniocnemis</i> (rare) |
| † <i>Oedipus rufescens</i> (moderate) | † <i>Lygosoma c. cherriei</i> (rare) |
| † <i>Hyla bocourti</i> (rare) | <i>Adelphicos v. veraepacis</i> (rare) |
| † <i>Hyla bromeliacia</i> (abundant) | † <i>Ninia s. sebae</i> (abundant) |
| <i>Hypopachus inguinalis</i> (rare) | † <i>Tantilla bairdii</i> (rare) |
| † <i>Anolis cobanensis</i> (rare) | † <i>Tantilla schistosa</i> (moderate) |

To what extent many of the members of the broadleaf forest fauna are indigenous to the pine area can only be conjectured. Several species secured in the pine area must be viewed as occasional visitants from the cloud forest. This is especially true of riparian types. Some well-established, true broadleaf forest species in the area, as several salamanders, may actually be recent immigrants from the cloud forest. The problem will be treated later in this paper.

The grassland habitat type in the pine area was probably originally only damp meadows (Pl. VII, Fig. 1). Species now found most abundantly in cornfields, cane fields, and pastures may represent in most instances tolerant species which inhabited the pine forest habitat type prior to the arrival of man. Second growth presents conditions not unlike those occurring in pine groves, while litter, as in cane fields, provides a habitat for species characteristic of the floor of the broadleaf forest. Species secured only in this habitat, *Corythophanes percarinatus*, *Drymobius chloroticus*, *Stenorrhina degenhardtii*, will undoubtedly eventually be taken in other habitats, especially the pine forest.

The grasslands assemblage includes:

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| <i>Bufo marinus</i> (abundant) | <i>Drymobius m. margaritiferus</i> (rare) |
| <i>Corythophanes percarinatus</i> (moderate) | <i>Adelphicos v. veraepacis</i> (moderate) |
| <i>Sceloporus m. taeniocnemis</i> (abundant) | <i>Ninia m. pavimentata</i> (rare) |
| † <i>Sceloporus teapensis</i> (rare) | <i>Stenorrhina degenhardtii</i> (rare) |
| <i>Gerrhonotus m. moreleti</i> (rare) | <i>Micrurus e. veraepacis</i> (rare) |
| <i>Drymobius chloroticus</i> (rare) | |

Though the largest body of standing water in Alta Verapaz is situated in the pine area at San Cristobal, (Pl. VIII, Fig. 2), the lenitic habitat is not a conspicuous feature of the life area. The lotic habitat, however, is both abundantly represented and uniformly distributed throughout the Meseta de Cobán (Pl. VII, Fig. 2). Despite the high development of the aquatic-riparian habitat types in the pine area, its associated fauna is not particularly outstanding. This may be because the bromeliad and forest-litter habitats compete with the aquatic environment for several amphibians, a situation which is rare on the lowlands.

The following make up the aquatic-riparian assemblage:

<i>Bufo marinus</i> (abundant locally)	† <i>Rana macroglossa</i> (abundant)
† <i>Eleutherodactylus brocchi</i> (abundant)	† <i>Rana pipens</i> (abundant)
† <i>Centrolenella fleischmanni</i> (moderate)	<i>Hypopachus inguinalis</i> (abundant)
† <i>Hyla baudinii</i> (rare)	† <i>Thamnophis e. fulvus</i> (rare)
† <i>Hyla spinipollex</i> (rare)	<i>Drymobius chloroticus</i> (rare)
† <i>Agalychnis moreletii</i> (moderate)	<i>Drymobius m. margaritifera</i> (moderate)
† <i>Plectrohyla quecchi</i> (moderate)	

The Cloud Forest life area, comprising about 8 per cent of Alta Verapaz, is the least known. It includes those areas above 1300 m. and occurs on the crests of the three mountain ranges extending eastward from the Meseta de Cobán and on the scattered mountains which surmount the Meseta itself. It is the only life area which lacks continuity in its distribution.

Studies within the cloud forest were carried on at fincas Samac, Chichén, and Volcán. The Mandel-Field Museum of Natural History expedition to Guatemala also made a small collection at Finca Samac. This is all of the herpetological material that has been obtained from the Alta Verapaz cloud forest, though it is believed that some of Bocourt's material (1865) came from this habitat (Stuart, 1948a: 8-9).

This life area is the most distinct of all the habitats in Alta Verapaz. Particularly characteristic features are high relief, abundant moisture, comparatively low temperatures with occasional frosts, continuous dense forest with low ground illumination, well-developed leaf mold and bromeliad habitats, and a sparsity of surface water (Pl. IX, Figs. 1 and 2).

From the cloud forest there have been recorded thirty species which include fourteen amphibians, six lizards, and ten snakes. Ten Quechian endemics occur in the life area and four of these are restricted to it. Six species are exclusive. Several additional forms appear to have recently emigrated from the cloud forest to the pine area, and it is possible that the region has recently received several immigrants from lower life areas.

There is nothing to show that the cloud forest supported anything other than a forest cover prior to human occupation. Whereas a grassland fauna

is well developed in the corozo area, an equivalent assemblage is only weakly defined in the cloud forest. In the corozo area the grassland habitat type is an older feature, whereas in the cloud forest it is a relatively recent cultural condition. The very nature of the physical environment of the cloud forest bears out this conclusion. The high humidity and low evaporation rate, owing to relatively low temperatures, more or less ensures heavy forest growth to the exclusion of natural grasslands. The humid conditions preclude destruction by fire and the absence of such killing factors as inundation probably eliminate any disturbances which might produce any wide distribution of a subclimax cover.

As in the forest of the corozo area no species displays a very high abundance in the cloud forest proper. The forest fauna is characterized by a number of leaf-mold and bromeliad inhabitants and is especially rich in those of leaf mold. This assemblage includes:

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| † <i>Oedipus helmrichi</i> (common) | † <i>Anolis nannodes</i> |
| † <i>Oedipus m. odonnelli</i> | <i>Gerrhonotus m. moreleti</i> (rare) |
| † <i>Eleutherodactylus anzueto</i> (rare) | <i>Rhadinaea hempsteadae</i> (common) |
| † <i>Eleutherodactylus bocourti</i> (rare) | † <i>Tropidodipsas kidderi</i> (common) |
| † <i>Eleutherodactylus stantoni</i> (rare) | † <i>Adelphicos v. veraepacis</i> (rare) |
| † <i>Eleutherodactylus xucanebi</i> (rare) | † <i>Imantodes c. leucomelas</i> (rare) |
| † <i>Hyla bromeliacia</i> (tadpoles indicate common) | † <i>Bothrops n. aurifer</i> (rare) |
| <i>Anolis cobanensis</i> (common) | † <i>Bothrops mexicanus</i> (common) |
| <i>Anolis c. haguei</i> (rare) | |

The grassland habitat type in the cloud forest is restricted to agricultural clearings and their accompanying second growth. Owing to the shallow soils and high relief which enhances soil erosion milpas are soon abandoned. In this zone there is far greater similarity of physical conditions between forest and grassland habitat types than there is between the same two habitats of the corozo area. The abundant rainfall ensures high humidity in the leaf-mold habitat even during the dry season, and the low-hanging cloud banks preclude constant exposure to direct sunlight and resulting high temperatures.

As a result of these factors, the more tolerant forest forms emerge to the more open habitats where their frequency is much higher than in the forest. This is a reversal of the situation in the Cahabón savannas, where the more tolerant grassland species invade the forest habitat type. Of the forms which were secured only in the grassland habitat type of the cloud forest, at least two, *Sceloporus m. taeniocnemis* and *Drymobius chloroticus*, give indication of being recent immigrants from the equivalent habitat of the pine area or coffee area. Others, such as *Eleutherodactylus brocchi* and *Ninia s. sebae*, and *Bothrops godmani*, also observed only in the grasslands habitat type, unquestionably occur in the forest but with such low abundance that they were understandably overlooked.

The grassland assemblage of the cloud forest includes:

<i>Eleutherodactylus brocchi</i> (abundant)	† <i>Drymobius chloroticus</i> (common)
<i>Anolis cobanensis</i> (common)	<i>Rhadinaea hempsteadae</i> (rare)
<i>Anolis c. haguei</i> (abundant)	<i>Ninia s. sebae</i> (rare)
† <i>Sceloporus m. taeniocnemis</i> (common)	<i>Bothrops godmani</i> (common)
<i>Gerrhonotus m. moreleti</i> (abundant)	

The aquatic-riparian habitat is but poorly developed in the cloud forest. The high relief of the area undoubtedly precludes any extensive development. Most of the streams are restricted to the lower margins of the life area (Pl. IX, Fig. 2) and the only standing water I saw was a dug water hole. Unlike some of the terrestrial amphibians, none of the aquatics are exclusive to the cloud forest.

The aquatic-riparian assemblage includes:

<i>Eleutherodactylus brocchi</i> (common)	† <i>Plectrohyla quecchi</i> (tadpoles indicate abundant)
† <i>Centrolenella fleischmanni</i> (rare)	
† <i>Hyla spinipollex</i> (tadpoles indicate abundant)	† <i>Rana macroglossa</i> (abundant)
† <i>Agalychnis moreletii</i> (rare)	† <i>Rana pipiens</i> (rare)
	<i>Thamnophis e. fulvus</i> (common)

The Coffee life area comprises 16 per cent of the Quecchian faunal area. Because it occupies a crossroads position between the corozo area of the lowlands and the pine and cloud forest areas of the highlands, its fauna is complexly and sporadically distributed. Furthermore, as will be shown, the statement of the local distribution of the fauna is far more subjective than is the case in other life areas.

The coffee area occupies the slopes of the three mountain ranges of Alta Verapaz between elevations of 600 to 1300 m. Major studies in the area were made by me at the fincas Panzamalá, Los Alpes, Volcán, and Chejel. Much of Alta Verapaz material preserved in various museums unquestionably originated in this same life area. It is fairly certain that the greater proportion of the specimens collected by Sapper came from Finca Campur (Stuart, 1948a:10).

The recorded fauna of the coffee area includes sixty-one species divided among fifteen amphibians, nineteen lizards, and twenty-seven snakes. Only one very poorly understood species is restricted to this life area, and but nine of the Quecchian endemics occur there.

The most conspicuous features of the coffee area are the high relief, sparsity of virgin cover, poor development of the lenitic environment, and tremendous altitudinal diversity in the composition of its fauna.

As indicated previously (Table II) there is, in this life area, a gradual vertical transition in the fauna, ranging from a high percentage and high abundance of lowland forms at the base of the region to a predominantly highland fauna in its upper parts. As a result, the mere statement of presence or absence of a species provides little information. *Hyla spini-*

pollex and *Plectrohyla quechchi*, for example, are members of its aquatic habitat only above 800 to 1000 m. Conversely, such species *Anolis l. bourgeai*, *Anolis sericcus*, and *Ameiva u. hartwegi* occur in the grasslands habitat type only below that level. In species ranging throughout the coffee area, there is often great discrepancy in their abundance at different elevations. Where sufficient data is available, therefore, altitudinal data should be included in the faunal lists.

Since the greater part of the accessible forests have been cleared from the coffee area to make room for coffee groves, it is difficult to give a clear picture of the forest habitat type and its fauna. Sometimes coffee groves may definitely be allocated to the forest habitat type, but the variation in shade at any one station is often so great that in many instances the reference of coffee groves to either the forest or the grassland habitat type is highly subjective.

In general the coffee area climax forest is much like the corozo area forest in physical features other than relief (Pl. VI, Fig. 1). The forest of the coffee area, however, has a far better developed leaf-mold habitat but lacks the continuity of distribution of that of the corozo area. Considering both the climax forest and coffee groves as presenting forest conditions, the forest habitat type occurs as islands within the grassland habitat type, which is the reverse of corozo area conditions. As a result there is less uniformity in the composition of the forest fauna from locality to locality than in the grassland assemblage in the coffee area. Heavily shaded coffee groves (Pl. VI, Fig. 2) appear to support the maximum development of the forest fauna especially with reference to leaf-mold and bromeliad (here largely restricted to banana plants) forms.

Species assigned to the forest fauna of the coffee belt are the following (the statement of abundance is a subjectively estimated mean for the indicated part of the coffee area occupied by each species) :

- † *Oedipus dofleini* (common)—below 1000 m.
- † *Oedipus elongatus* (rare)—below 700 m.
- † *Oedipus m. odonnelli* (abundant)—above 1000 m.
- † *Oedipus rufescens* (abundant)—600–1300 m.
- Eleutherodactylus rugulosus* (rare)—below 1000 m.
- † *Anolis nannodes* (rare)—above 1250 m.
- Corythophanes cristatus* (rare)—below 700 m.
- Lygosoma c. cherriei* (common)—below 1300 m.
- Ninia s. sebae* (abundant)—upper limit unknown
- † *Tantilla schistosa* (common)—below 1300 m.
- Micrurus a. apiatus* (common)—below 1200 m.
- Micrurus e. veraepacis* (common)—below 1300 m.
- † *Bothrops mexicanus* (common)—upper limit unknown

The grasslands habitat type in the coffee area includes lightly shaded coffee groves, cornfields, pastureland, and the dense second growth that

follows abandonment of cultivated land. It is doubtful if a natural grasslands habitat ever existed to any great extent in the coffee area. The closest approach to such is the scattered pine cover that occurs locally on some of the shallow-soiled, steep slopes of the upper Polochic Valley.

The problems involved in determining the nature of the forest fauna of this life area are also true of the grassland assemblage. The deep litter of open coffee groves provides conditions suited to forest forms, which further confuses the ecological picture.

Most of the specimens secured from the grasslands habitat type were in lightly shaded *cafetales*. Rank second growth and pastures present the same problems of study in the coffee area as were noted in the discussion of the corozo area.

Insofar as any unbiased analysis can be made of the grasslands assemblage the following forms may be allocated to it:

- Bufo marinus* (abundant)—below 1300 m.
- Bufo valliceps* (abundant)—below 1200 m.
- † *Anolis biporcatus* (rare)—below 1000 m.
- † *Anolis l. bourgeai* (abundant)—below 900 m.
- † *Anolis cortezi* (rare)—limits unknown
- † *Anolis l. rodriguezii* (abundant)—below 1200 m.
- † *Anolis sericeus* (rare)—below 700 m.
- Basiliscus vittatus* (common)—below 1000 m.
- † *Sceloporus teapensis* (abundant)—below 1300 m.
- Lepidophyma f. flavomaculatum* (common)—below 900 m.
- Lygosoma c. cherriei* (common)—below 1300 m.
- † *Ameiva u. hartwegi* (abundant)—below 1000 m.
- † *Drymobius chloroticus* (rare)—upper limit unknown
- Drymobius m. margaritiferus* (abundant)—below 1300 m.
- Dryadophis m. laevis* (common)—below 1300 m.
- † *Spilotes p. mexicanus* (common)—below 1300 m.
- † *Drymarchon c. melanurus* (rare)—below 1100 m.
- † *Thalassophis m. mexicanus* (common)—below 1000 m.
- Lampropeltis t. abnorma* (common)—below 1300 m.
- Phocercus e. salvinii* (common)—below 1300 m.
- Ninia s. sebae* (abundant)—upper limit unknown
- Imantodes c. leucomelas* (rare)—upper limit unknown
- Micrurus a. apiatus* (common)—below 1200 m.
- Bothrops a. asper* (common)—below 1100 m.

Species secured in the grasslands habitat type which are not definitely a part of the typical fauna include:

- Gymnopsis oligozona* (rare)—below 900 m.
- Typhlops tenuis* (rare)—below 1300 m.
- Scaphiodontophis a. annulatus* (rare)—below 1300 m.
- Rhadinaea d. decorata* (rare)—below 900 m.
- Tropidodipsas s. sartorii* (rare)—below 1100 m.
- Stenorrhina degenhardtii* (rare)—below 1300 m.

The aquatic-riparian habitat type is here almost as poorly developed as it is in the cloud forest and Cahabon savannas. The high relief limits the lenitic habitat to artificial "tanks," occasional small ponds, and a few hillside marshes formed by springs. Though the lotic habitat type might be expected to reach its maximum development, seasonal rainfall and the porous substructure produce only seasonal flow in the majority of the streams. Lack of water during the dry season is a serious problem on many coffee plantations. As a result the aquatic-riparian assemblage is represented by but eleven forms. This fauna includes:

- Bufo marinus* (abundant)—below 1300 m.
- Bufo valliceps* (abundant)—below 1200 m.
- Eleutherodactylus rugulosus* (rare)—below 1000 m.
- † *Centrolenella fleischmanni* (abundant)—upper limit unknown
- † *Hyla baudinii* (abundant)—below 1250 m.
- † *Hyla spinipollex* (tadpoles indicate abundant)—above 800 m.
- † *Agalychnis moreletii* (rare)—above 800 m.
- † *Plectrohyla queechi* (tadpoles indicate abundant)—above 800 m.
- Rana pipiens* (abundant)—below 1300 m.
- Basiliscus vittatus* (rare)—below 1000 m.
- Drymobius m. margaritiferus* (rare)—below 1300 m.

Two somewhat specialized minor habitats, the "bromeliad-banana" and the "leaf-mold" habitats, are worthy of somewhat detailed treatment. Both occur naturally but have been considerably modified through human occupation, and certain anomalies of animal distribution in Alta Verapaz have resulted.

The bromeliad habitat, characterized by the well of water at the base of the plant and the film of moisture between the overlapping leaves, not only presents a continuously moist environment for secretive arboreal forms but actually extends the lenitic habitat into upper forest stories. So far as is known none of the Alta Verapaz reptiles or amphibians makes use of the "well" of the bromeliads, thus the film of moisture present between the overlapping leaves of the banana plant presents comparable conditions to those in the bromeliad. For that reason the term "bromeliad-banana" may be applied to the habitat.

The bromeliad-banana habitat was undoubtedly best developed in the cloud forest prior to human occupation. Since the great expansion of coffee cultivation, however, in which the banana is utilized for shade, today this environment has its peak development in the coffee area.

Table III lists the species known to occur in the bromeliad-banana habitat of Alta Verapaz together with several Alta Verapaz species that have been observed in the same type of environment in adjacent regions. In addition, it would not be surprising to find *Centrolenella fleischmanni*, *Sphaerodactylus lineolatus*, and *Dipsas dimidiatus* in the habitat. It is true that many of these species are merely arboreal forms which may seek

only temporary refuge in the habitat. Nevertheless, as predators or prey of other bromeliad-banana habitat species, they represent a vital part of the fauna. This list of twenty species compares most favorably with bromeliad assemblages reported from adjacent regions. Dunn (1937) has recorded fourteen such species from Costa Rica and Smith (1941) seventeen from Mexico.

TABLE III
MEMBERS OF THE BROMELIAD-BANANA FAUNA OF ALTA VERAPAZ

Species	Life Area Inhabited	Remarks
<i>Oedipus helmrichi</i>	Pine area, cloud forest area	
<i>Oedipus mulleri</i>	Pine area	
<i>Oedipus odonnelli</i>	Upper coffee area	
<i>Oedipus rufescens</i>	Coffee area, pine area, Cahabón savanna area	
<i>Hyla baudinii</i>	Tropical zone	Occurs sporadically
<i>Hyla bocourti</i>	Pine area	
<i>Hyla bromeliacia</i>	Pine area, cloud forest area	
<i>Hyla loquax</i>	Corozo area	Occurs sporadically
<i>Hyla staufferi</i>	Corozo area	Smith, 1941: 38
<i>Agalychnis callidryas</i>	Corozo area	Occurs sporadically
<i>Agalychnis moreletii</i>	Coffee area, pine area, cloud forest area	Occurs sporadically
<i>Sphaerodactylus glaucus</i>	Corozo area	Smith, 1941: 43
<i>Anolis nannodes</i>	Coffee area, pine area	
<i>Anolis pentapirion</i>	Corozo area	Smith, 1941: 42
<i>Thalerophis m. mexicanus</i>	Corozo area, coffee area	Smith, 1941: 39
<i>Sibon nebulatus</i>	Corozo area	Dunn, 1937: 164
<i>Tropidodipsas kidderi</i>	Cloud forest area	
<i>Imantodes c. leucomelas</i>	Tropical and Subtropical zones	
<i>Leptodeira a. polysticta</i>	Corozo area	
<i>Bothrops n. aurifer</i>	Cloud forest area	

The bromeliad-banana fauna is unevenly distributed both temporally and areally. Discovery of large colonies of a species by one collector in a given area may not coincide with the experience of another collector in an adjacent region of similar physical conditions. Smith secured large series of *Oedipus rufescens* during the dry season at Potrero Viejo, Veracruz (Taylor and Smith, 1945: 548), while during the same season in Alta Verapaz I was able to collect but a comparatively meager number of that species.

Norman Hartweg collecting on Mount Ovando in Chiapas found bromeliads particularly barren of fauna during the wet season (verbal communication). Smith working the same mountain during the dry season collected as many as thirty-eight salamanders from a single plant (Smith, 1941: 43).

While there is at present no logical explanation to account for regional discrepancy in the faunal population of bromeliads, it seems indicated that seasonal variation is merely a response to humidity. Amphibians, particularly, appear to seek the moist situation of the bromeliad and the banana during the often severe dry season in northern Central America.

The bromeliad fauna of Alta Verapaz was areally unevenly distributed. In the Lower Tropical zone only *Imantodes c. leucomelas* and *Leptodeira a. polysticta* of the true bromeliad assemblage were secured. Some years ago in the Petén to the north of Alta Verapaz I had found the bromeliad habitat similarly barren. So far as seasonal differences in the corozo area were concerned, none was discovered. The coffee area with its abundance of planted bananas proved somewhat more fruitful, but even there the fauna was by no means uniformly distributed. At Panzamalá I secured nothing from either bromeliads or bananas. At Los Alpes *Oedipus rufescens* was fairly abundant in the bananas. Volcán, however, proved very rich compared with the other two localities, but the fauna was localized, and only in the higher coffee groves at altitudes between 900 and 1300 m.

Seasonal variation in the abundance of species secured in the habitat in Alta Verapaz was noticeable but not so well marked as that observed in other regions. This was probably because the commoner species of the fauna appear to pass their entire lives in the bromeliad habitat. Certainly the oedipi listed in Table III were never secured elsewhere regardless of season. Although little is known of the life history of oedipine salamanders, Taylor and Smith (1945: 543, 549) observed in Mexico eggs on September 17 and December 12, and young in July. This suggests wet-season breeding activities. If such is the case, it is only natural that the bromeliad oedipi would reach their minimum population during the first part of the wet season and would occur in considerable numbers at the end of the wet season and into the dry season.

Although the planted banana leads to the greatest development of the bromeliad-banana habitat in the coffee belt, the pine belt supports the largest resident bromeliad-banana fauna. The more humid broadleaf forests do not, apparently, impose upon their faunas excessively xeric conditions. The open and drier pine forest of the Meseta de Cobán, together with its high relief and extensive subterranean drainage, presents a seasonally arid habitat. In fact the relief and subterranean-drainage features alone probably explain the extensive development of the bromeliad assemblage at elevations above 900 m. It may be noted that the species which are strictly bromeliad-inhabiting are largely highland forms. This suggests that intolerance to high temperature in addition to water requirements may restrict the true bromeliad species to higher elevations in Alta Verapaz.

So far as is known, only a single bromeliad-inhabiting species in Alta Verapaz has undergone any extensive modification to fit it for bromeliad life. This species, *Hyla bromeliacia*, which has an elongate and flattened tadpole, I have already described (Stuart, 1948a: 30-31, Figs. 3-4).

The leaf-mold habitat is less widely distributed than the bromeliad-banana habitat. In the Lower Tropical zone, where conditions of high humidity and temperature exist, decay of organic matter is so rapid that

leaf mold rarely accumulates on the forest floor, except for spaces between the buttresses of the larger trees where considerable debris may accumulate. Under natural conditions in the Upper Tropical zone decay is somewhat retarded by lower temperatures, yet humus, except under special conditions, is not a conspicuous feature of the forest floor. In the Subtropical zone, however, leaf mold is abundant.

As a result of human occupancy humus accumulation is best developed in the coffee groves, as described by Slevin (1939: 398). In Alta Verapaz the groves are cleared of vines, grass, and superfluous banana plants, and these, with trimmings from coffee bushes, are generally raked into long rows

TABLE IV
MEMBERS OF THE LEAF-MOLD FAUNA OF ALTA VERAPAZ

Species	Life Area Inhabited	Remarks
<i>Oedipus dofleini</i>	Coffee area	
<i>Oedipus elongatus</i>	Coffee area	
<i>Bufo valliceps</i>	Corozo area, coffee area	Occasionally present
<i>Eleutherodactylus anzeutoi</i> ...	Cloud forest area	
<i>Eleutherodactylus bocourti</i> ...	Cloud forest area	
<i>Hypopachus inguinalis</i>	Pine area	
<i>Lygosoma c. cherriei</i>	Coffee area, pine area	
<i>Ehadinaea hempsteadae</i>	Cloud forest area	
<i>Adelphicos q. visoninus</i>		Cane fields at La Primavera
<i>Ninia diademata</i>		Cane fields at La Primavera
<i>Ninia s. sebae</i>	Tropical and Sub-tropical zones	
<i>Coniophanes i. clavatus</i>		Cane fields at La Primavera
<i>Tantilla schistosa</i>	Tropical zone except Cahabón savannas	
<i>Micrurus e. veraepacis</i>	Corozo area, coffee area, pine area	

or into conical piles. Within about two-months time this debris has rotted to form a loosely consolidated, spongelike mass which even at the height of the dry season provides a moist habitat (Pl. IV, Fig. 2). When first gathered into piles the rubbish is not sufficiently compact to afford proper life conditions for the leaf-mold fauna; after about three months it becomes overgrown with grass and is too solid. As a result the habitat is short-lived, but the cleaning of the coffee groves is a more or less continuous process, so the leaf-mold assemblage always finds a suitable habitat at its disposal in the coffee and pine areas.

In cacao groves and small plots of coffee in the corozo area and the Cahabón savannas, the leaf-mold habitat is present but poorly developed. In the cloud forest, which is above the limits of coffee cultivation, this habitat occurs naturally on the forest floor.

Table IV lists the species comprising the leaf-mold community of Alta Verapaz together with several species secured in the same type of habitat at La Primavera in the Zacapan biotic province. Although they have not been secured in leaf mold, *Gymnopsis oligozona*, *Typhlops tenuis*, and *Micrurus a. apiatus* are undoubtedly members of the community. Slevin (1939:414) reported *Pliocercus e. elapoides* (= *Pliocercus e. diastemus*), which is a close relative of the Alta Verapaz *Pliocercus e. salvinii*, from mulch piles in the coffee groves of southern Guatemala (El Ciprés).

Like the bromeliad-banana fauna, the leaf-mold assemblage was not uniformly distributed. Slevin secured eleven species of reptiles in the habitat at El Cipres as compared with but eight definitely reported from Alta Verapaz. In Alta Verapaz there was considerable discrepancy in the abundance of certain species from place to place. The population was largest in the coffee and pine areas where the habitat is best developed. *Ninia s. sebae* the commonest member of the fauna was secured in the following numbers in different life areas in the Quecchian biotic province:

Life Area	Corozo Belt	Coffee Belt	Pine Belt	Cloud Forest
Specimens	3	14	17	1

This was not owing to difference in the time spent in collecting; about the same amount was devoted to turning over leaf mold in each of the life areas.

There was variation also in the size of the leaf-mold population from place to place at similar elevations. Dry-season collections of *Ninia s. sebae* from four localities yielded the following numbers of individuals:

Locality	Los Alpes	Volcán	Panzamalá	Samac
Specimens	0	4	9	17

The largest population noted was that of the cane fields (1120 m.) at La Primavera. The workmen of that finca brought me almost two hundred specimens of *Ninia s. sebae* picked up within a single day. Unfortunately, the great majority were so badly mangled or decayed as not to warrant preservation. The cane fields at Samac proved to be disappointingly sterile.

Even within a single coffee grove, where rubbish was all in about the same stage of decay, areal differences in the population were marked. Only one type of mulch appeared to be definitely avoided, that in which rotting banana plants occurred.

Little seasonal variation was noted in the leaf-mold fauna. In the Quecchian province there was a slightly larger population in the humus during the dry season. Yet the tremendous series of *Ninia s. sebae* found at La Primavera was secured over a month after the wet season had begun.

The habitat may have greatly modified the local abundance of species, but there is little evidence that the mulch piles have upset these virgin distributional patterns. It appears rather that the frequency of the habitat in the coffee and pine belts has merely tended to produce a large and concentrated population of several of the species which have undoubtedly always been present in those life areas.

Though both the bromeliad-banana and leaf-mold habitats occur under extant condition in both the forest and grassland habitat types, there is little question but that their assemblages, under natural conditions, are basically forest aggregates. Only under artificial conditions, as lightly shaded coffee groves, do these environments flourish in the grassland habitat type.

INFLUENCE OF MAN. To what extent the picture presented in the foregoing mirrors natural conditions can only be surmised. The extensive distribution of a small but distinct grassland assemblage in the Tropical zone, a region which in prehuman times was unquestionably, with slight exception, heavily forested is an enigma strongly suggestive of considerable departure from the virgin geographic pattern. Again the abundance of bromeliad-inhabiting species in the pine life area where bromeliads are normally sparse is strikingly paradoxical. It may be worthwhile, therefore, to examine briefly these and other apparently enigmatic observations and to essay an explanation. Other faunal paradoxes in Alta Verapaz include the frequent occurrence of the same Alta Verapaz endemics in both the pine and cloud forest life areas, regions of very dissimilar environmental characters, and the abundance of leaf-mold-habitat species in the pine and coffee life areas as opposed to their rarity in virgin forests of both the corozo and cloud forest life areas.

In preface to a discussion of these anomalies, it must be indicated that, despite a lack of detailed information, it is becoming increasingly apparent that two different terrestrial faunal assemblages have evolved in or invaded Central America, a grassland assemblage and a forest assemblage. In the Tropical zone these two assemblages are represented by the following conspicuous examples:

GRASSLAND ASSEMBLAGE

Anolis limifrons subsp.
Anolis lemurinus subsp.
Anolis sericeus subsp.
Basiliscus vittatus
Sceloporus, variabilis group
Ameiva undulata subsp.
Dryadophis melanolomus subsp.
Drymarchon corais subsp.
Masticophis m. mentovarius
Oxybelis fulgidus

FOREST ASSEMBLAGE

Eleutherodactylus, rhodopsis group
Anolis humilis subsp.
Ameiva festiva subsp.
Thalerophis occidentalis subsp.
Ehadinæa decorata subsp.
Bothrops, mexicanus group
Bothrops, nasutus group

Subtropical zone species are still too poorly known to give similar definite lists of species, but *Anolis crassulus* subspecies and *Thamnophis eques* subspecies appear to be more grassland types than the strictly forest-inhabiting *Oedipus helmrichi* (or *dunni*) group or *Bothrops godmani*.

That both these major assemblages are represented in Alta Verapaz indicates that in prehuman times Alta Verapaz supported the grassland as well as the forest habitat type. The impoverished condition of the lowland grassland assemblage (see p. 25 for a list of typical Petén grassland species absent from Alta Verapaz) suggests that the assemblage was either restricted in its distribution, or fairly effectively isolated from more extensive grasslands to the north and east by forest barriers, or both. The Cahabón savannas with the endemic species *Ameiva chaitzami* represents a grassland area which may have served as a center from which a grassland assemblage radiated when suitable habitats became available. Moreover, short-lived grassland habitat types resulting from burns, inundation, and other natural causes may have acted as stepping stones through a forest barrier. It seems certain that the more tolerant grassland species followed such routes through the forests and into the Cahabón savannas from natural grasslands to the north and east, those of the Petén and Honduras, respectively.

There is little question but that the forest habitat type occupied most of Alta Verapaz in prehuman times. It remained only for specialized environments to develop to increase greatly the abundance of certain species or to extend the ranges of others into regions superficially, at least, rather unfavorable to the true forest assemblage.

By comparing areas of virgin cover with those which have been modified by cultivation it seems apparent that such anomalous geographic conditions as may be observed in Alta Verapaz have stemmed in relatively recent times from the impact of two culturally diverse groups upon the natural landscape. These two are the Indian with his subsistence farming, milpa agriculture, which on the lowlands dates from possibly 1000 B.C. (Morley, 1946: 44), and the European with his commercial agriculture, which was not greatly expanded in the region until after the dawn of coffee planting, about 1850. Milpa agriculture, characterized by clearing, planting, and abandonment within but a few years, has been the more effective in extending the grassland habitat type. Coffee cultivation while sometimes producing a grassland habitat type of greater permanency, that is, pastures, lightly shaded coffee groves, etc., has in other instances produced a forest environment in the coffee groves, with the banana plants as shade (the ecological equivalent of bromeliads) and with the deep mulch layer resulting from cleaning the groves. This has even further extended the broadleaf forest habitat into the pine life area. Thus, the two diverse agricultural activities may have

produced faunal rearrangements both through extermination and through extension of ranges.

The primary clearing operations could have caused considerable local extermination. The forest fauna in particular appears to have suffered, with deaths resulting from burning as well as from such modifications in the environment as increased light, decreased humidity, destruction of food supply, and temporary restriction of range. Nevertheless, it is doubtful that any member of the Alta Verapaz herpetofauna has been entirely exterminated owing to this factor. More probably it has reduced the numbers of some species locally and thus unbalanced the natural picture insofar as conclusions based upon short-time investigations are concerned. Certainly the spotty distribution of some forest species is strongly suggestive of extensive destruction of the forest habitat type.

After the actual clearing, the planting of milpas and lightly shaded coffee groves or the production of permanent pasture land has greatly extended the grassland habitat type and its fauna, especially in the corozo and coffee life areas. Both these areas were forest environments in pre-human times, yet today, especially in the east, much of the Tropical zone supports a grassland habitat type and herpetofauna. The lack of such items as *Anolis l. rodriguezii*, *Sceloporus teapensis*, and *Ameiva u. hartwegi*, in the western and northwestern parts of the Tropical zone exhibits only too clearly less extensive cultivation and an isolation from the grassland environment of the east. The occurrence of such species as *Sceloporus m. taeniocnemis* and *Thamnophis e. fulvus* in the clearings of the dense cloud forest suggests a slight invasion of that life area by unquestionably exotic grassland species.

Present distributions indicate that the broadleaf forest habitat type has primarily been extended only into the pine life area where coffee groves and their associated bananas have produced broadleaf forest conditions out of a virginally open-forest (pine) environment. It is suspected, for instance, that certain cloud-forest species, notably *Oedipus helmrichi*, *Hyla bromeliacia*, and *Anolis nannodes* are recent immigrants into the broadleaf coffee groves of the pine life area. It is worthy of note that, although collectors during the 1860's and 1870's secured in the Cobán region such rarities as *Hyla bocourti* and *Bothrops n. aurifer*, they failed to discover such now abundant species as *Oedipus helmrichi* and *Hyla bromeliacia*. These two species are bromeliad-inhabiting forms which have taken over the banana plants as a habitat in the older coffee groves.

In both the coffee and pine life areas the heavy mulch cover of the coffee groves presents a habitat which is only poorly developed in virgin forests. As a result, as an environment for secretive types, this exceeds in favorableness that of the virgin forest and the associated fauna has flourished in

proportion. Though it is questionable that any normal ranges have been modified by these advantageous conditions, the natural abundance of such a species as *Ninia s. sebae* has been locally greatly increased.

Despite these and other possible geographic modifications resulting from cultural impacts, the major pattern outlined in the preceding geographic account is probably still fairly representative of the virgin pattern. If there has been any change, it would appear that the several life areas and their associated faunas have become less clearly defined as the natural landscape has been modified. It is conceivable, for instance, that the six species now restricted to the cloud forest life area may have been double that number in prehuman times, whereas the fauna of the pine life area might have lacked these same six species. It is fortunate that there still remains in Alta Verapaz a sufficiently extensive disposition of virgin or near-virgin conditions to enable us to understand, in their major outlines at least, the nature of the zoogeographic patterns in this most complex area.

In summarizing the foregoing ecological data the following points are of especial significance:

1. Two distinct herpetofaunal elements, a highland and a lowland, are recognizable in Alta Verapaz.

2. Although constituting only about 25 per cent of the herpetofauna, no less than 80 per cent of the Alta Verapaz endemism is restricted to the highland element and but one endemic is confined to the lower zones.

3. Three major herpetofaunal assemblages occur in each of the several life areas of Alta Verapaz, the grassland assemblage, the forest assemblage, and the aquatic-riparian assemblage. The aquatic-riparian assemblage, owing to the fact that its constituents are in a large measure drawn from adjacent habitat types, is of little value as an indicator of the fundamental assemblage types of the Alta Verapaz herpetofauna.

4. Of the terrestrial reptiles and amphibians concerning which there is adequate ecological data (about 50 per cent of the total herpetofauna), roughly 45 per cent are restricted to the forest habitat type, 25 per cent are restricted to the grassland habitat type, and the remainder are forms which, though occurring in both habitats, show a marked partiality to the environment of the forest.

5. Of the analyzed part of the terrestrial endemics (sixteen), nine are restricted to the forest habitat type, one to the grassland habitat type, and six though appearing to favor the forest habitat occur in both habitats.

From these essential data the following conclusions have been drawn:

1. The highlands, that is the Subtropical zone, have not proven a favorable environment for the several faunal elements which have entered Alta Verapaz.

2. In showing considerable differentiation, it is indicated that the highland assemblage, especially the strictly forest species, has been associated with a highland environment over a more extensive period of time than has the lowland assemblage.

3. The forest fauna in showing a greater degree of endemism is probably of somewhat greater age than the grassland fauna both in the highlands and at lower elevations.

It is upon these facts that an unraveling of the historical aspects of the Alta Verapaz herpetofauna will be based.

ORIGIN OF THE HERPETOFAUNA

I noted at the beginning of this geographic account that, in addition to the static faunal presentation, I would essay a dynamic account of the historical aspects of the Alta Verapaz herpetofauna. In giving motion to the descriptive material presented in the foregoing, the data are not only interpreted but also crystallized into a general summary. Pertinent to the unraveling of the origin of the Alta Verapaz herpetofauna is an appraisal of the position of both the region and its fauna in the more extensive picture of northern Central America as a whole.

There is no little disagreement among specialists concerning the history of the region. It is generally conceded, however, that with the exception of some of the low borderlands to the north and east, Alta Verapaz has been, as a minor unit of nuclear Central America, a positive area throughout the entire Cenozoic. This entire nuclear mass has been separated, probably, from both North and South America at different times during the Cenozoic. Though Schuchert (1935) suggested isolation of South America from late Eocene through mid-Miocene, recent investigations by Olson and McGrew (1941) in Honduras extend this isolation of the southern continent until late Pliocene. A second portal, that of Tehuantepec, isolated Central America from North America. Here again specialists are not in accord. Schuchert suggested an open Tehuantepec portal from late Miocene through early Pliocene, but Olson and McGrew suggested an earlier closure of that interoceanic strait. Insofar as an accounting for the various faunal elements in northern Central America is concerned the exact dating of these open portals is of minor importance. Yet its isolation at one time or another from both the north and south—and from the south over a fairly extensive period—is requisite to an accounting for the nature of the northern Central American herpetofauna.

With respect to the herpetofauna, one may first examine it in the light of its affinities. Dunn's (1931) now classic arrangement of the herpetofaunal elements of the Americas reveals that the Alta Verapaz assemblage is composed entirely of Old Northern and South American elements. Ac-

cording to his scheme, the family groupings of Alta Verapaz representatives would be as given below :

OLD NORTHERN	SOUTH AMERICAN
Plethodontidae	Caeciliidae
Bufonidae	Leptodactylidae
Ranidae	Hylidae
Dermatemydidae	Microhylidae
Kinosternidae	Gekkonidae
Chelydridae	Iguanidae (in part)
Emydidae	Teiidae
Iguanidae (in part)	Leptotyphlopidae
Xantusidae	Boidae
Scincidae	Colubridae (in part)
Anguidae	
Xenosauridae	
Typhlopidae	
Colubridae (in part)	
Micruridae	
Crotalidae	

In scoring this arrangement it will be noted that of twenty-four families represented in the herpetofauna of Alta Verapaz, fourteen are Old Northern, eight are South American, and two were subjected to independent evolution on both sides of the lower Central American portal. These last, however, may, on a historical basis, be grouped with the Old Northerners insofar as their northern representatives are concerned. According to this scheme, the Alta Verapaz generic count might run slightly in favor of the Old Northerners. Owing to the fact that several of the genera are in need of evolutionary study, no exact placement of all can be made at this time, but the proportion would probably stand in the neighborhood of forty to thirty.

In my opinion, however, a slight rearrangement of Dunn's scheme would give the herpetofauna an even more pronounced Old Northern hue. Dunn has suggested that no less than four of the families represented in the Alta Verapaz herpetofauna (Gekkonidae, Iguanidae, Typhlopidae, and Colubridae) may have been present on both sides of the lower Central American portal during the period of continental separation. The occurrence of certain endemic genera of South American affinities in Middle America would seem to indicate that additional families or subfamilies may have been subjected to a similar dual history.

Among the amphibians *Agalychnis* and *Plectrohyla* of the Hylidae suggest such a situation, while *Hypopachus* among the microhylids appears to be another parallel. Though Burt (1931: 251-56) is in definite opposition to such an opinion, the rather considerable differentiation in *Cnemidophorus* in the north could conceivably add the Teiidae to this group. An especially large group of xenodontine colubrids (South American in Dunn's scheme)

seem to be representative of the same. The following Alta Verapaz genera may be noted.

<i>Rhadinaea</i>	<i>Ninia</i>
<i>Coniophanes</i>	<i>Adelphicos</i>
<i>Pliocercus</i>	<i>Conophis</i>
<i>Tropidodipsas</i>	<i>Amastridium</i>

The *Dendrophidion-Drymobius-Dryadophis* complex and the genus *Simophis* suggest that the Colubrinae might have had representatives in northern South America, where they developed during the period of continental isolation.

The history of the Middle American group of genera with South American affinities is still very obscure. Some, such as the *Rhadinaea-Coniophanes* complex, suggest nuclear Central America as their center of origin, whereas Dunn (*in litt.*) would support the "Panama-Baudó" island as a center for *Agalychnis* which might also serve for the colubrine *Dryadophis* complex as well. Furthermore, we cannot even be certain that the genera mentioned above arose from relict prototypes that were stranded in Middle America following continental separation. It is entirely possible that they are recent entrants from South America which have undergone explosive evolution. Such an explanation is indicated by two Mexican leptodactylids, *Tomodactylus* and *Microbatrachylus*, but the majority of the genera with which I have been concerned are sufficiently well defined to suggest somewhat longer histories as entities. Finally, there is little data to contradict the supposition that certain herpetofaunal elements have engaged in island-hopping, as suggested by Simpson (1940) for several mammalian groups. If such were the case a history similar to, but of longer duration than, that of the true South Americans would be indicated rather than the Old Northern-like history that I have previously inferred.

Though such a suggestion is possibly premature, it may be noted that, owing to their South American rather than North American affinities, an autochthonous Middle American element of varied histories may be singled out and added to Dunn's basic faunal classification.

If, for the sake of argument, the above remarks may be acceptable, the herpetofauna of Alta Verapaz, historically speaking, would become strongly Old Northern or Old Northern-like. A rough count might reveal a generic proportion of possibly two to one in favor of the Old Northerners over the South Americans. The value of such an arrangement would be found in its bearing upon our efforts to explain the extensive and often very local differentiation that may be observed in many portions of northern Central America. In Alta Verapaz, for example, it would reveal that with the exception of such highly plastic genera as *Hyla* and *Eleutherodactylus*, local differentiation is confined entirely to those genera of an Old Northern-like history. The importance of this fact will be brought out later.

Basically then, the Alta Verapaz herpetofauna is Old Northern in its broader aspects. In a more detailed study such as this paper purports to be, however, such a generalization can hardly suffice as an account of the faunal history.

The several herpetofaunal elements as defined by Dunn and slightly rearranged in the above, have come together in various combinations to produce in northern Central America, and particularly in Guatemala, three herpetofaunal assemblages. These are the Caribbean assemblage, the Pacific assemblage, and the Plateau assemblage.

These three are not of equal value, but, rather, the first two might be grouped as a unit of lowlanders as opposed to the third which is a highland unit.

The lowland assemblages are rather less lowland in their distribution than in their origin and extant affinities insofar as northern Central America is concerned. While a few of the genera such as *Eleutherodactylus*, *Hyla*, *Anolis* (in part), and *Dryadophis* may range up into the Subtropical zone along humid slopes, the great majority, notably *Leptodactylus*, the turtles and crocodiles, *Basilisus*, the teiids, and many colubrids (*Spilotes*, *Drymarchon*, *Thalerophis*, *Dipsas*) are restricted to the Tropical zone. Whenever genera are represented in both the lowland and the highland assemblages, differentiation of subgeneric degree, at least, characterizes the representatives in the two assemblages (*Bufo*, *Anolis*, *Bothrops*).

It is perhaps too early to try to define the lowland faunas with any degree of exactness. It can be said that the Pacific assemblage differs from that of the Caribbean primarily in its impoverishment. A rough estimate might show that the former is possibly only two-thirds the size of the latter. Among the Caribbean genera not represented on the Pacific lowlands of Guatemala are the following:

<i>Hypopachus</i>	<i>Celestus</i>
<i>Dermatemys</i>	<i>Storeria</i>
<i>Claudius</i>	<i>Dendrophidion</i>
<i>Chelydra</i>	<i>Pseustes</i>
<i>Sphaerodactylus</i>	<i>Tretanorhinus</i>

In addition to these genera are others which are represented by but a single species on the Pacific coast of Guatemala as compared with several on the Caribbean side. Especially notable are *Kinosternon*, *Ameiva*, *Coniophanes*, *Stenorrhina*, while *Hyla*, *Anolis*, and *Bothrops* are all much better developed on the Caribbean side than on the Pacific.

On the other hand a few genera are more characteristic of the Guatemalan Pacific lowlands than of the Caribbean. Restricted to the Pacific lowlands are *Caiman* (on the Caribbean only to Nicaragua), *Loxocemus*, *Ungaliophis*, and *Trimorphodon*, while *Geophis* and *Gymnophthalmus* barely enter the Caribbean area.

Some genera are represented on either lowland area by different species groups; *siniferus* group versus the *variabilis* group among the ground scelopori or the *nigrocinctus* complex versus the *apiatus* series in *Micrurus*. Finally, a group of species shows subspecific differentiation in the two lowland areas, for example *Anolis* (the majority of these have not as yet been recognized), *Ameiva undulata*, *Drymobius margaritiferus*, *Tropidodipsas sartorii*, *Lampropeltis triangulum*, *Pliocercus elapoides*, and many others.

Yet despite these dissimilarities there is considerable unity in the lowland faunas of northern Central America and viewed *in toto* this major assemblage is strikingly different from the plateau fauna.

The plateau fauna is characterized by excessive impoverishment. From the highlands of southwestern Guatemala, for instance, only twenty species belonging to thirteen genera are known. Lowland elements not entering these uplands have already been mentioned. A few genera are restricted to these higher elevations, notably *Plectrohyla*, *Xenosaurus*, and *Gerrhonotus*. The remainder of the highland species belong to groups which are very different from those occupying the lowlands or are, in almost every case, well-differentiated species. Here may be included the *formosus* group of *Sceloporus*, the *godmani* group of *Rhadinaea*, and the *fisheri* group of *Tropidodipsas*, while *Bufo bocourti*, *Anolis crassulus*, and *Bothrops godmani* have no apparent lowland relatives.

The lowland assemblages are made up of the several faunal elements previously discussed in approximately the same proportions as noted for Alta Verapaz, that is, two to one, in favor of the Old Northerners over the South Americans. The plateau assemblage is composed exclusively of true Old Northerners (*Oedipus*, *Gerrhonotus*, *Thamnophis*) or Old Northern-like genera of South American affinities (*Plectrohyla*, *Rhadinaea*, *Tropidodipsas*).

The Alta Verapaz herpetofauna is predominantly of the lowland type. Exemplified by *Bufo marinus*, *Hyla baudinii*, *Basiliscus vittatus*, and *Constrictor c. imperator*, all the lowlanders, with the exception of *Trimorphodon* are typical Caribbean species. It is significant that *Trimorphodon* is restricted to the subhumid Cahabón savannas in Alta Verapaz. Not more than 10 per cent of the Alta Verapaz herpetofauna is of highland origin and none of that group descends below 800 m.

We are concerned, therefore, primarily with faunal assemblages whose affinities fall into two distinct groups, one that is characteristic of the lowlands of northern Central America and one that is generally associated with the plateau lands of the same area. The history of the Alta Verapaz herpetofauna, therefore, may be expected to parallel with minor variations the history of those two major assemblages in northern Central America as a whole.

Schmidt (1943) has shown that various faunal waves have spread through the inter-American isthmian region while other groups have remained stranded in the northern section as "hanging relicts" in what he has termed a faunal "paleopeninsula." It remains, then, only to apply Schmidt's general principles to the Alta Verapaz subdivision of that more extensive area and to elaborate some of the details associated with the faunal development in this more localized life area. In unraveling the herpetofaunal history of Alta Verapaz we must often resort to "degree of differentiation" in the several faunal elements represented. Owing to such variable factors as plasticity, tolerance, rate of movement, and others, consideration of the "degree of differentiation" may often lead to conclusions of questionable validity, but the fact remains that in northern Central America as a whole, the greatest local differentiation in the herpetofauna is encountered among those groups which have inhabited the region over the longest period of time, or have been subjected to the greatest amount of modification, or both.

The first faunal wave to enter Central America swept in from the north prior to the close of the Eocene period. The greater part of this wave moved southward into South America where, between late Eocene and possibly early Pliocene times, it evolved into the South American element (*sensu* Dunn). As suggested, a part of that fauna (Hylidae, Gekkonidae, Iguanidae, etc.) may have remained stranded in the isthmian region during the period of continental separation, or may have moved northward by island-hopping during that same period.

Following this wave came a second, Dunn's more ancient Old Northerners which were now unable to move farther southward than nuclear Central America owing to the open lower Central American portal.

On the lowlands and moderately elevated uplands in a forest and scattered grasslands environment (Olson and McGrew, 1941) in this southwestern peninsula of North America, representatives of these two early faunal elements were undergoing generic evolution. From the prototypes of the first evolved, either in Central America or on the Mexican Plateau, such genera as possibly *Agalychnis*, *Hypopachus*, *Basiliscus*, *Laemactes*, *Rhadinaea*, and *Coniophanes*, and from the second developed *Oedipus*, *Xenosaurus*, *Scaphiodontophis*, *Micrurus*, *Bothrops*, and others.

As the period of South American isolation came to a close, three events came into play to upset Central American faunal tranquillity. First, a break of short duration between North and Central America developed in the Tehuntepec region, possibly during late Miocene times. Second, world refrigeration was gradually developing. Third, the Pliocene orogeny elevated to high altitudes much of nuclear Central America. These three factors working together molded the extant herpetofauna of northern Central America in general and of Alta Verapaz in particular.

Isolation from North America permitted further differentiation in the Central American herpetofauna concurrent with evolution which witnessed the genesis of such genera as *Sceloporus*, *Thamnophis*, and *Crotalus* on the Mexican Plateau. World cooling accompanied by extensive uplift in northern Central America appears to have caused a split in the *in situ* herpetofauna of that region and to have initiated its division into a highland and a lowland group. Some indication of the extent of uplift during the Pliocene and subsequent times is indicated in the occurrence of Miocene sediments at above 7500 feet elevation in Chiapas (Schuchert, 1935: 325). Thus before the close of the Pliocene there probably was present in Alta Verapaz and the adjacent regions such groups as the following:

1. Lowlanders

Oedipus, mexicanus group
Agalychnis
Hypopachus, cuneus group
Testudinata
Basiliscus
Corythophanes
Laemactus
Lygosoma
Scaphiodontophis
Rhadinaea, decorata group
Coniophanes
Pliocercus
Tropidodipsas, sartorii group
Leptodeira
Micrurus
Bothrops, mexicanus, nasutus,
 and *atrox* groups

2. Highlanders

Oedipus, dunni group
Plectrohyla
Hypopachus, inguinalis
 group
Gerrhonotus, deppii group
 (?) *Xenosaurus*
Rhadinaea, godmani
 group
Tropidodipsas, fischeri
Bothrops, godmani group

With the temperature reductions that accompanied the closing of the Tehuantepec portal the southward movement of the younger Old Northern element from the Mexican Plateau was initiated. Griseom (1932:25) has suggested that during the height of Pleistocene glaciation the Subtropical zone of Guatemala was reduced to sea level. Insofar as the herpetofauna is concerned, there is little evidence that the Tropical zone was completely eliminated from northern Central America. Such excessive chilling would unquestionably have brought about widespread extermination among lowlanders, yet we know definitely that the area served as a refuge for many ancient lowland types, notably the turtles. Furthermore, the tropical South American element would probably have been barred from the same region. The extant abundance of that element, however, suggests a history certainly longer than post-Wisconsin in northern Central America.

At any rate it is indicated that, some time during the Pliocene, there was initiated a dual invasion of northern Caribbean Central America by two diverse faunal elements, the South American and the younger Old

Northern. The South American followed the now somewhat more extensively emerging lowlands, whereas the younger Old Northern flowed southward along two distant routes, a highland or highland slope route and a lowland (the Yucatán Peninsula) route. It is further indicated that several waves moved along these routes at different times, but there is too little evidence to permit the full substantiation of this possibility.

Those Old Northerners following the highland route, *Sceloporus malachiticus*, *Gerrhonotus*,* and possibly *Thamnophis* in part, now mixed with the more ancient highlanders previously noted, some of which had apparently already undergone local differentiation in the highlands of Alta Verapaz. But it was not until the close of the last glaciation when the Subtropical zone was elevated to its present height that such barriers as the Río Negro gorge and the interior desert basins could act as isolating mechanisms to enhance differentiation in Alta Verapaz among the younger Old Northern element. Thus today among the more ancient Old Northerners or Old Northern-like groups there is fairly complete specific differentiation: *Oedipus helmrichi*, *Plectrohyla quecchi*, *Rhadinaca hempsteadae*, and *Tropidodipsas fischeri*. In the younger group, on the other hand, differentiation is either lacking or at best is subspecific: *Sceloporus m. taeniocnemis*, *Gerrhonotus m. moreleti*, and *Thamnophis e. fulvus*.

The lowland entrants into the Alta Verapaz region, both from the south and north, remained confined to the lowlands until fairly recent times. Only a few of these have invaded the highlands of Alta Verapaz to the subtropical level. In a few instances slight differentiation in the highland populations has taken place, practically all of it in Old Northern groups. The following may be noted:

ALTA VERAPAZ FORM	LOWLAND ANCESTORS
<i>Oedipus m. mulleri</i>	<i>Oedipus m. mexicanus</i>
<i>Oedipus m. odonnelli</i>	<i>Oedipus m. mexicanus</i>
<i>Oedipus dofleini</i>	<i>Oedipus yucatanus</i>
<i>Eleutherodactylus bocourti</i>	<i>Eleutherodactylus spatulatus</i>
<i>Eleutherodactylus xucanebi</i>	<i>Eleutherodactylus alfredi</i>
<i>Dryadophis m. laevis</i>	<i>Dryadophis m. alternatus</i>
<i>Lampropeltis t. abnorma</i>	<i>Lampropeltis t. polyzona</i>
<i>Micrurus a. apiatus</i>	<i>Micrurus a. alienus</i>

Finally, it may be noted that, especially insofar as the northern element is concerned, invasion of Alta Verapaz was accomplished first by a forest assemblage and more recently by a grassland assemblage. Certainly in its size and differentiation the forest group gives evidence of having been resident in the area over a greater length of time than has the grassland group.

* Since this was written, Tihen (1949) has suggested an earlier invasion of Central America by the gerrhonotids. Such an assumption, while supportable, is hardly necessary to explain the presence and differentiation of that group in Central America.

CONCLUSIONS

Owing to an absence of herpetofaunal studies of areas comparable to the Alta Verapaz, the preceding account must stand, until such time as similar studies are forthcoming, as simply an effort to apply the broader herpetological principles of Dunn (1931) and Schmidt (1943) to a local faunal assemblage in an effort to explain its make-up and history.

In analyzing the region and its fauna *intra se* and by comparing it with adjacent areas, notably the Sierra de los Cuchumatanes, the Petén, and the Plateau of Guatemala, several general principles may be established. First, the herpetofauna of northern Central America is overwhelmingly of a lowland type. With few exceptions, only the more ancient inhabitants of the region have been able to cope with the reduced temperatures that stemmed from the combination of recent uplift and world refrigeration. Second, recent invasion of the highlands of Guatemala by lowland groups has been restricted almost entirely to those uplands of mesic conditions. The herpetofauna of the localized humid Subtropical zone of Alta Verapaz is, for instance, almost 30 per cent greater than that of the relatively extensive but subhumid Plateau of Guatemala. Third, in a region of such complex environmental and faunal histories as the Alta Verapaz, extant environmental differences and local isolation do not suffice to explain the differentiation or lack of differentiation in the herpetofauna. Only through an analysis of the various historically different faunal elements considered in the light of the history of the environment can the nature of the herpetofauna be understood. Finally, the local zoogeographic pattern appears to have stemmed from the impact of a number of local and the often fortuitously coincidental arrangements of environmental factors upon the diverse faunal elements which have invaded the region. For this reason it is doubtful if that pattern and the analysis of its causal agencies would be applicable to other regions. The region is of interest, however, primarily because its several local environments run the gamut of most of the major environments encountered elsewhere in northern Central America, and because its fauna appears to illustrate in detail some of the more generalized faunal conclusions that have been formulated previously.

SUMMARY

1. Alta Verapaz represents a natural area composed of a highland limestone block with adjacent low borderlands, which through faulting and erosion or solution has been broken into three orographic units invaded by or surrounded by four lowland units.

2. With the exception of the slightly subhumid Cahabón Valley, Alta Verapaz is a region of high humidity and rainfall and has an average annual temperature of 25° C. on the lowlands. At the higher elevations a zone of occasional frosts is encountered.

3. The various orographic and climatic features produce five vegetation zones: a tropical area including broadleaf forest and local savannas at low elevations; broadleaf forest and pine forest at higher elevations; and above 1300 m., a subtropical cloud forest.

4. The varied life requirements of the diversified herpetofauna render it difficult to show that any single environmental factor is a controlling distributional agent. Nevertheless the fortuitous coincidence of a number of such factors permits the recognition of several major environmental types within the region.

5. The herpetofauna of Alta Verapaz is composed of 129 forms of reptiles and amphibians, of which about 20 per cent are endemic.

6. Through comparisons with the herpetofauna of adjacent regions, it is shown that the Alta Verapaz herpetofauna comprises a distinctive assemblage occupying a faunal region which has been named the Quecchian (Stuart, 1942, 1943a).

7. Through increasingly more detailed analysis, it is concluded that five distinct herpetofaunal assemblages occupy, in Alta Verapaz, as many life areas, which are roughly coincidental with the five major vegetational zones.

8. Available data are sufficiently detailed to permit recognition of but three herpetofaunal agglomerations within each of the five life areas. These are the "grassland," the "forest," and the "aquatic-riparian" assemblages.

9. A brief description of the environment and the several herpetofaunal assemblages of each of the life areas is presented.

10. A somewhat extended discussion of two specialized habitats, the "leaf-mold" and the "bromeliad-banana" habitats is presented. In some instances these are dependent largely upon cultural modifications in the natural landscape.

11. It is concluded that the impact of Indian and European cultures, while producing considerable modification in the natural landscape, has not destroyed the basic zoogeographic pattern that existed in prehuman Alta Verapaz.

12. Available ecological data indicate that the herpetofauna of Alta Verapaz is basically a lowland, forest type. Endemism is encountered primarily in the highland assemblage.

13. The Alta Verapaz herpetofauna has arisen from several elements which have developed *in situ* in northern Central America or have invaded it in several waves from the north and south.

14. Continental connection or isolation to the north and south coupled with the Pliocene orogeny of northern Central America and world refrigeration during the Pleistocene appears to have been the most active agent in molding the nature of the Alta Verapaz herpetofauna.

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PLATE I



FIG. 1. The foothills of the Sierra de Pocolhá. Finca Chamá, June, 1938.



FIG. 2. The lower Polochic Valley eastward from above the junction of Río Polochic and Río Panimá. February, 1940.

PLATE II



FIG. 1. Dense second growth on the flood plain of the Río Polochic near Panzós. February, 1940.



FIG. 2. Cultivated areas on the northern lowlands. Finca Cubilguitz, July, 1938.

PLATE III



FIG. 1. Woodland pond in the deep rain forest of the northern lowlands, Finca Seboquil, July, 1938.



FIG. 2. Inundations of the eastern lowlands by the Río Polochic, several kilometers to the south (background). Panzós, September, 1940.

PLATE IV



FIG. 1. *Sigüan* or sink in the second growth at Finca Samac. The brush had to be cut back to expose this opening. April, 1938.



FIG. 2. Raking in the decayed mulch in a coffee grove. Finca Panzamalá, March, 1938.

PLATE V



FIG. 1. Entrenchment of the Río Cahabón near Finca Canihor, April, 1940.



FIG. 2. Rocky hillsides of the Cahabón savannas. Finca Los Pinales, August, 1938.

PLATE VI



FIG. 1. Trail through virgin forest along the border of the Coffee and the Cloud forest life areas. Finca Panzamalá, March, 1938.



FIG. 2. Trail through a coffee grove at Finca Los Alpes, March, 1940.

PLATE VII



FIG. 1. Northward across the pine forests on the Meseta de Cobán. Finca Chichén, June, 1940.



FIG. 2. Pine groves along the headwaters of the Río Cahabón on the Meseta de Cobán near Cobán. August, 1940.

PLATE VIII

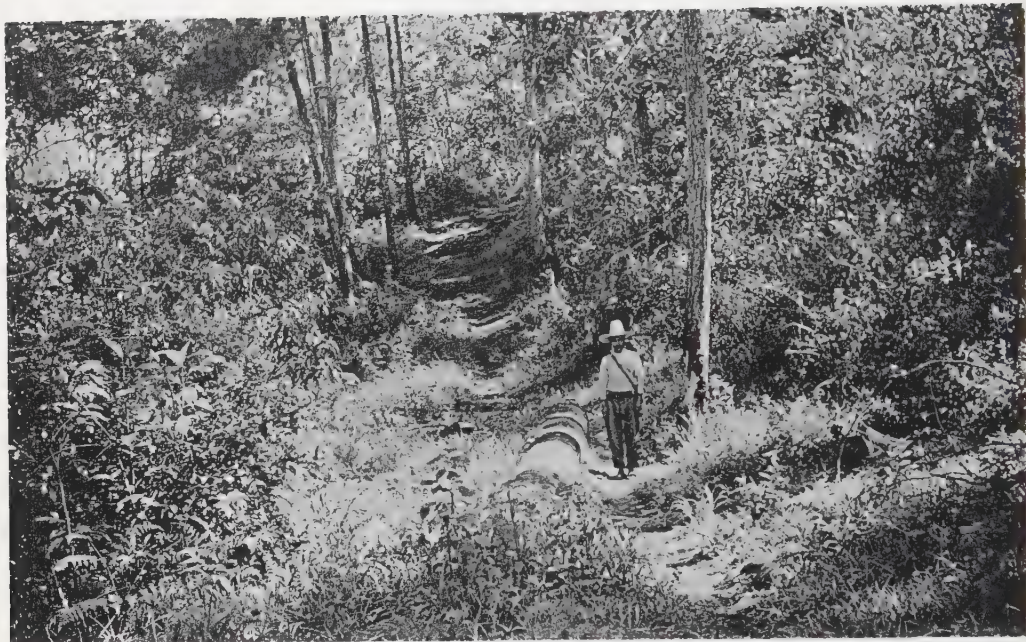


FIG. 1. Trail through a pine forest at Finca Chichén. June, 1940.



FIG. 2. Cornfield in the Pine life area. Laguna San Cristobal in the middle background is the largest body of water in Alta Verapaz. Cloud forest on ridges in far background. August, 1938.

PLATE IX



FIG. 1. New clearing in the cloud forest on the ridges above Finca Samac. May, 1938.



FIG. 2. Stream at the base of the cloud forest at Finca Chichén. May, 1940.

